POST-CONFLICT BEHAVIOUR AND RELATIONSHIP QUALITY OF CERCOPITHECINE PRIMATES

Duncan Lorimer Castles

A Thesis Submitted for the Degree of PhD
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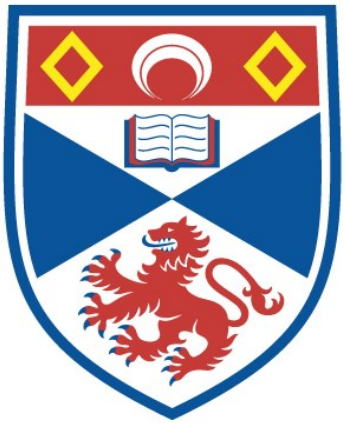
University of St Andrews



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Dissertation submitted to the University of St Andrews for the degree of Doctor of Philosophy

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ABSTRACT

This thesis investigates the nature of post-conflict behaviour and relationships among individuals in two captive groups of pigtail macaques, *Macaca nemestrina*, and one wild troop of olive baboons, *Papio anubis*. Data were collected during periods of seven and twelve months respectively.

In both pigtail groups, conflicts were more frequently reconciled between opponents with strong affiliative ties. However, reconciliation was twice as common in the well-established group where individuals' social networks were more compact. It is argued that the more intense ties produced by restricted networks increased the likelihood of reconciliation.

Reconciliation was demonstrated among wild olive baboons, occurring at a rate consistent with a relatively intolerant dominance style. Opponents who were close kin or of similar rank reconciled relatively frequently, but reconciliation rarely followed conflicts associated with food. Olive baboons did not 'console' each other, consistent with the hypothesis that consolation requires an ability to empathise with victim distress. Initiation of post-conflict attacks on third parties was not elevated in victims of aggression.

Among the baboons, both victims and initiators of aggression exhibited elevated rates of post-conflict self-directed behaviour (a combined measure of scratching, autogrooming, body-shaking and yawning). Reconciliation reduced both SDB and the incidence of further aggression. However, reconciliation only reduced SDB among individuals involved in conflicts in which they had both received and delivered aggression.

Female baboons showed significantly higher rates of SDB when their nearest neighbour (within 5 m) was a dominant conspecific than when he or she was a subordinate individual, supporting the hypothesis that SDB indexes stress in primates. This result suggests that SDB can be used to index relationship security in primates.

MULTIPLE AUTHOR MANUSCRIPTS

This thesis includes three multiple author journal manuscripts. All data analysed in these manuscripts were collected by me (except some ad libitum data used for the construction of dominance hierarchies). The initial idea of comparing the dominance style of the two pigtail groups was Frans de Waal's. Otherwise, I was predominantly responsible for 1) the project design, 2) the design and execution of analyses, and 3) the writing of the manuscripts.

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The versions of manuscripts included in this thesis have benefited from the comments of many of the individuals mentioned above. They have also been hugely improved by the contributions of several anonymous reviewers, Robin Dunbar, Volke Sommer and the sterling editing of Angela Turner and Kate Lessells.

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CONTENTS

Chapter 1. INTRODUCTION

The ultimate function of an animal's behaviour is to maximise its inclusive fitness (e.g. Dawkins 1982, 1989). Fundamentally, this is dependent on obtaining adequate access to energy providing resources. When groups are formed, animals may benefit from reduced predation risk, communal rearing, improved defence of and/or acquisition of resources (e.g. Dunbar 1988). However, because group-living animals are surrounded by competitors for key resources, they also suffer increased competition. Thus, an individual's ability to obtain resources is constrained by its interactions with, and the behaviour of, other group members.

In social environments, behavioural interactions between individuals can have consequences for their reproductive success (Pusey & Packer 1997). During interactions, individuals can obtain information about their partners' propensity to co-operate or their competitive ability which can influence future interactions. Individuals may also act in such a way as to affect each other's prospects of survival and reproduction. The content, patterning and quality of interactions between two individuals can be described as a relationship (Hinde 1979, 1983). Since the characteristics of relationships have implications for inclusive fitness, there is expected to be selection on individuals to manipulate relationships in their best interests (Kummer 1978; Byrne & Whiten 1988). Indeed this manipulation can extend beyond the individual's own relationships to the relationships held by other group members (de Waal 1982; Cheney & Seyfarth 1990).

Relationships, then, are at the core of primate societies, they are both critical components of the social environment and strategic means of managing and handling that environment, ultimately to the individual's self-interest. Consequently, students of animal societies need to develop their understanding of animal relationships to improve their comprehension of animal societies. Conventionally, two measures of social interaction have been employed. Aggression between individuals, because it carries costs of dispersion, stress and danger, has been used as a marker of relatively poor

quality relationships, while affiliation, non-aggressive social interaction such as allogrooming, embracing and passive contact associated with a range of utilitarian and social benefits, has been used as a marker of relatively high quality relationships.

For the past two decades, attention has been directed towards extended aspects of aggression and affiliation among primates. A large research effort has identified a range of post-conflict behaviours, such as *reconciliation* and *consolation*, which have profound implications for our understanding of aggressive behaviour (e.g. de Waal 1989b; Kappeler & van Schaik 1992; de Waal & Aureli 1996). More recently, extensive research into displacement activity, apparently irrelevant behaviour patterns associated with states of motivational conflict, has been re-evaluated and employed as support for a proposal that displacement activities may be effective measures of stress and emotionality in non-human primates (e.g. Schino et al. 1988; Maestripieri et al. 1992). In tandem with simple affiliative measures these have the potential to radically increase the power of relationship quality indices.

In this thesis, I examine aspects of the nature of aggression and affiliation in cercopithecine primates. Specifically, I examine the behaviour of three groups of cercopithecine primates: two captive groups of pigtailed macaques, *Macaca nemestrina*, and a wild group of olive baboons, *Papio anubis*, paying particular attention to 1) Post-conflict behaviour: the details of patterns of behaviour following aggressive interactions and their relationship to other social parameters, and to 2) Displacement, or 'self-directed', behaviour: stress related behavioural patterns which I examine in conjunction with affiliation and aggression to gain insight into the emotions of primates engaging in social interaction and to better characterise their relationships.

In this chapter, I briefly review previous work on primate social relationships, post-conflict behaviour and self-directed behaviour in order to place the current study in perspective. This is followed by an outline of the remainder of the thesis.

Describing primate societies

Primate societies are the products of interactions between the individuals who constitute a society. Such interactions are the behavioural components of primate social relationships (Hinde 1979, 1983). There are two predominant approaches to the analysis of social relationships among primates. Hans Kummer (1978) emphasised the functional repercussions of investing in social relationships. His concept is of a relationship as an investment which enables beneficial social interactions. Ultimately benefit is expressed in individual reproductive success. Interactions can, of course, be immediately beneficial, such as allogrooming to remove ectoparasites and clean the skin (Freeland 1981; Hutchins & Barash 1976), but, critically, they also serve to shape relationships to maximise the value of a social partner. For example, if X grooms Y frequently, Y may support X in agonistic interactions, reciprocate by grooming X frequently, or protect X's offspring.

Robert Hinde (1976, 1979, 1983) used the term relationship to describe the content, pattern and quality of interactions between two individuals. These parameters delineate the way in which individuals respond, and have previously responded to one and other. Hinde utilised this theoretical approach in a multi-leveled exposition of primate societies which has become paradigmatic to the analysis of primate relationships. At the base, are patterns of interactions between individuals, which are used to describe and characterise the relationships of individuals. In turn, patterns of relationships are used to describe and compare groups or societies.

A component of both Kummer and Hinde's definitions is that later interactions are influenced by earlier ones and thus, by definition, relationships persist over time. Significantly, both approaches - which are complimentary - emphasise the importance of relationships; they are at the heart of primate social order. A relationship is both a component of the social structure, an element of the social environment in which it exists, and a strategic tool which an individual employs to manage reproductive success. They are thus of fundamental importance to any analysis, description and

study of primate sociality, and any discipline or study which seeks to draw conclusions from the form of primate societies. Given such importance, the problem for researchers becomes one of how to study and measure primate relationships, and a variety of measures of positive and negative dimensions of relationship quality have been employed. Such measures range from the simple, such as measures of aggression and affiliation rate, to the complex (e.g. Drews 1993), which can be problematic to apply to differing taxa or ecological conditions.

Simple measures have the advantage of replicability and easy generalisation but, unfortunately, they can lack subtlety which compromises their continued success. As mentioned above, the relative frequency of aggression has been employed as a measure of relationship quality. Since aggression is costly because it can lead to displacement from resources, prolonged activation of the stress response, high energetic demand, and injury (Smuts 1987), individuals are expected to refrain from inflicting such costs on valued social partners. Thus, relationships marked by high rates of aggression are considered to be of low quality. Unfortunately, the reality of the expression of aggression is somewhat different, at least among cercopithecine primates. Primates are expected to invest in those relationships which have the most potential benefit to them (Kummer 1978; Cords & Aureli 1993; Cords 1997), therefore the relationships of kin-related animals should be of high quality because related individuals can benefit not just indirectly, by exchanging resources or social favours (e.g. de Waal 1989a), but also directly, by investing in close relatives (Hamilton 1964). However, a number of studies indicate that rates of aggression are in fact highest among kin (e.g. Japanese macaques: Kurland 1977; vervet monkeys: Horrocks & Hunte 1983; rhesus macaques: Bernstein & Erdhart 1986).

Similarly, other measures of relationship quality suffer problems. Allogrooming, and time spent in contact or close proximity are examples of a constellation of behaviours associated with stress reduction (Terry 1970; Boccia 1989) alongside other beneficial utilitarian (Hutchins & Barash 1976) and social functions (Sade 1972; Lindburg 1973). Thus, elevated rates of

active affiliation have been taken to index high relationship quality. Yet, to note the problems of just one of those dimensions, affiliation neither invariably nor uniformly reduces physiological measures of stress (Boccia et al. 1989). Moreover, it can even be accompanied by elevated levels of stress in participant individuals (e.g. Sapolsky 1993). Both factors compromise the efficacy of employing affiliative rate as a direct measure of relationship quality.

Undoubtedly a major aspect of the problem is that social primates may affiliate for multiple reasons. Relationships can be characterised on at least three dimensions - value, security and compatibility (Kummer 1978; Cords & Aureli 1993). In Cords & Aureli's terminology, *value* refers to the benefits which can be derived from a relationship; *compatibility* to the accessibility of the partner, i.e. if they are often nearby in the group or have a history of friendly interaction; *security* to the predictability of a relationship - the extent to which an individual can expect its partner to behave in a given fashion. This approach to primate relationships provides a framework for distinguishing relationships according to the motivation of participants. For example, an animal of high value may receive high rates of affiliation even though its partner does not perceive the relationship as a secure one. Equally, that partner may direct similar rates of affiliation toward a third, less valuable individual because its relationship with that individual is considerably more secure.

By measuring affiliation rates alone we are limited to a reliable measure of relationship compatibility alone. To better describe primate relationships a measure of relationship security is necessary. As security captures the predictability of relationships it can, in principle, be assessed by measuring how comfortable an individual is with a conspecific; assuming that individuals will be most comfortable or relaxed in the presence of partners whose behaviour is most predictable. Therefore, behavioural measures of an individual's emotional state could enable us to distinguish differing levels of security.

In this thesis I intend to use the findings of two areas of ethological research to more accurately utilise aggression and affiliation as measures of

relationship quality. I hope to demonstrate that the post-conflict behaviour of individuals involved in aggression provides valuable information on relationship quality. Similarly, I intend to show that affiliative measures can be illuminated by attending to behavioural indicators of stress in combination with more traditional measures. I will now briefly discuss the literature relevant to these two areas.

Post-conflict behaviour

Among social animals, intra-group resource competition is largely unavoidable and, as a result, social conflict is inescapable (van Schaik 1989). While aggression is neither the only form, nor an inevitable expression, of social conflict (Mason 1993), it is the most obvious manifestation of resource competition (Walters & Seyfarth 1987). Aggression is dispersive, stressful and dangerous (Smuts 1987). However, in some non-human primates species, certain behaviours which occur in the period after aggressive conflict appear to have evolved to dissipate the negative consequences of aggression. These include: 1) *reconciliation*: peaceful interaction between former opponents; 2) *redirection*: the attack of a formerly uninvolved individual by the target of the initial aggressive incident, and 3) affiliative interactions between a former opponent and individuals uninvolved in the original conflict, including *consolation* and *substitute reconciliation*.

Reconciliation

Reconciliation was the term used by Frans de Waal & Anton van Roosmalen (1979) to label selective affiliative interaction which occurred between former opponents soon after aggression. While there were several prior anecdotal reports of friendly interactions following aggression in chimpanzees, langurs, and macaques (Sade 1965; Blurton-Jones & Trollope 1968; van Lawick-Goodall 1968; Nishida 1970; Seyfarth 1976; McKenna 1978), formal investigation of primate post-conflict behaviour began with de Waal and van Roosmalen's study of the Arnhem Zoo chimpanzees, *Pan troglodytes*. Their research has blossomed into a significant field of

primatological and ethological research with its own international research group, workshops at scientific meetings and popular presentations for the non-specialist audience.

A critical factor in the emergence of this area of academic discourse was the development of a research methodology enabling the detection, description and analysis of post-conflict behaviour. De Waal and colleagues realised that it was important to confirm that former opponents are more likely to affiliate in the period following agonistic conflict than they are in periods without agonistic conflict; i.e. that affiliation is increased following conflicts. The methods introduced to study the conciliatory behaviour of rhesus macaques, *Macaca mulatta*, (de Waal and Yoshihara 1983), involving a comparison of the latency to affiliation in the immediate post-conflict period (PC) to that in a matched-control period (MC), provided the template for numerous later studies. The PC and MC are focal observations of one of the former opponents, commonly of 10 minutes duration, designed to be matched to each other in all respects except occurrence of conflict (see methods section of Chapters 2 & 4 for further details). There have been several minor objections and alterations to de Waal and Yoshihara's methods concerning, for example, the precise criteria for selection of MCs; duration of PCs and MCs; spatial positioning; ongoing activity; which behaviours should be regarded as conciliatory; and the calculation of reconciliation rate (e.g. Kappeler & van Schaik 1992; Cords 1993; Veneema et al. 1995; Koyama 1997), but the basic methodology persists and drives virtually all studies of the conciliatory behaviour of primates and other taxa. To summarise, for the demonstration of increased post-conflict affiliation a variety of methods suffice. However, problems can emerge when calculating conciliatory tendency and comparing rates across studies, groups or species, as differences in methods and, indeed, differing natures of species must be considered.

Formal investigations of post-conflict interactions now encompass at least 20 primate species including rhesus (de Waal & Yoshihara 1983; Thierry 1986; de Waal & Johanowicz 1993; Call et al. 1996; Smucny et al. 1996), long-tailed, *M. fascicularis* (Thierry 1986; Cords 1988, 1992; Aureli et

al. 1989; Aureli & van Schaik 1991a, b; Aureli 1992, in press; Cords & Aureli 1992; Cords & Thurnheer 1993; Aureli et al. 1997; Das submitted), Tonkean, *M. tonkeana* (Thierry 1986), stumptail, *M. arctoides* (de Waal & Ren 1988; de Waal & Johanowicz 1993), Japanese, *M. fuscata* (Thierry 1990b; Aureli et al. 1993, 1997; Chaffin et al. 1995; Koyama 1997), pigtail (Judge 1991), Barbary, *M. sylvanus* (Aureli et al. 1994, 1997), crested, *M. nigra*, (Petit & Thierry 1994a), and moor macaques, *M. maurus* (Matsumura 1996); sooty mangabeys, *Cercocebus atys* (Gust & Gordon 1993); Guinea, *P. papio* (Petit & Thierry 1994b) and chacma baboons, *P. ursinus* (Cheney et al. 1995; Silk et al. 1996); patas, *Erythrocebus patas* (York & Rowell 1988), vervet, *Cercopithecus aethiops* (Cheney & Seyfarth 1989, 1990), golden, *Rhinopithecus roxellanae* (Ren et al. 1991) and brown capuchin monkeys, *Cebus apella* (Verbeek & de Waal 1995); ring-tailed, *Lemur catta*, and brown lemurs, *Eulemur fulvus* (Kappeler 1993); bonobos, *Pan paniscus* (de Waal 1987) and mountain gorillas, *Gorilla gorilla beringei* (Watts 1995a, b). Just one of these studies failed to demonstrate increased rates of non-agonistic behaviour between former opponents in the period following a conflict (brown lemurs, Kappeler 1993). Many have also demonstrated that increases in post-conflict affiliation were selective; directed, in the main, to the former adversary - *selective attraction* (*sensu* de Waal & van Roosmalen 1979). In addition, some attention has been paid to assessing the conciliatory mechanisms of other taxa. Friendly interactions between former opponents following aggression have been observed in a number of non-primate species (mouflon, *Ovis ammon*: Pfeffer 1967; spotted hyena, *Crocuta crocuta*: Kruuk 1972; East et al. 1993; lion, *Panthera leo*: Schaller 1972; dwarf mongoose, *Helogale undulata*: Rasa 1977; feral ram, *Ovis aries*: Rowell & Rowell 1993).

While many of the above mentioned studies have limited their scope to a description of post-conflict behaviour the overriding goal of ethological study is to understand how and why behaviour occurs. To this end, there has also been considerable discussion of the function of conciliatory behaviour from both ultimate and proximate perspectives.

The ultimate function of conciliatory behaviour

Generally, researchers have attempted to understand the function of conciliatory behaviour by linking the expression and frequency of reconciliation to other aspects of the study animal's behavioural repertoire. Several variables have been invoked as predictors of reconciliation frequency. These include 1) the decidedness of the original conflict - higher rates of reconciliation following undecided conflicts are predicted; 2) the directionality of the original conflict - higher rates of reconciliation following bi-directional or conflicts initiated against the hierarchy are anticipated; and 3) the distance between combatants in the dominance hierarchy - reconciliation is expected to be more frequent when opponents are of similar rank (Thierry 1986, 1990a; Aureli et al. 1989; Judge 1991; Petit & Thierry 1994a, b). The evidence to support such theories in one species is frequently contradicted by data from other studies and/or the effects can be more parsimoniously explained by alternative hypotheses.

A more promising approach is that the frequency of reconciliation depends on the quality of relationships between opponents, especially their value (the 'relationship quality' hypothesis: de Waal & Yoshihara 1983; Aureli et al. 1989; Kappeler & van Schaik 1992). In species with highly co-operative matrilineal kin relationships, related individuals tend to reconcile more often than unrelated ones (Aureli et al. 1989, 1997; Thierry 1990b; Judge 1991; Call et al. 1996). Conciliatory interactions increased dramatically following conflict between pairs of long-tailed macaques that had learned to collaborate to obtain food (Cords & Thurnheer 1993). While chimpanzee males form alliances with one another that serve both within- and between-group competition, while females have relatively loose relationships; accordingly conflicts between males are more often reconciled than those between females (Goodall 1986; de Waal 1986). In mountain gorillas where males are important to females both as social partners and as protectors, conflicts between females and adult males are reconciled but conflicts with immatures or other females are not (Watts 1995a).

Recently, Joan Silk (1996) has taken issue with the theory that conciliatory interactions function to repair relationships damaged by conflicts. She argues that 'peaceful post-conflict contacts', as she prefers to label them, are merely signals of benign intent which enable former opponents to re-establish peaceful contact. She also contends that conciliatory interactions have no long term consequences for the relationships of individuals who participate in them because a study of female chacma baboons found that such interactions had no consistent effect on the frequency of social interaction in the ten days following a conflict (Silk et al. 1996). However, as Cords & Aureli (1996) point out in a reply to Silk's article, it is quite consistent for conciliatory interactions to be both signals of benign intent at the proximate level and to serve to repair relationships at the ultimate level. Moreover, reconciliation need not increase the frequency of affiliation in the days following a conflict for it to be said to have repaired a relationship; rather if reconciliation enables affiliation to return to pre-conflict levels it can be said to have repaired the relationship (even if it does not entirely restore affiliation levels but enables higher levels than there would have been had there been no post-conflict interaction, it can still be said to have improved the relationship). Indeed, in a recent study of free-ranging Japanese macaques, Koyama (1997) demonstrated that the rate of affiliation between former opponents in the ten days following a conflict was restored to pre-conflict levels by reconciliation but was significantly lower than pre-conflict levels if reconciliation did not occur.

The proximate function of conciliatory behaviour

By employing self-directed behaviour (SDB) as a measure of anxiety (see below), studies of captive longtailed macaques have demonstrated that the victims of aggression experience elevated levels of stress in the immediate post-conflict period (Aureli et al. 1989; Aureli & van Schaik 1991; Aureli in press; de Waal & Aureli in press). These studies also demonstrate that post-conflict conciliatory interactions between victims and their former opponents reduced victims' stress to the level of non-conflict periods.

Smucny et al. (1996) report that aggression increases, and reconciliation reduces, heart rate in rhesus macaques. This work has led to the development of the 'uncertainty reduction' hypothesis (Aureli & van Schaik 1991): that following conflicts, victims are stressed because they are uncertain as to the future behaviour of their opponent and other group members, from whom they are likely to receive further aggression, and their uncertainty and stress is manifest in increased rates of SDB. Reconciliation reduces the risk of receiving further aggression, reducing victims' uncertainty. Therefore, the proximate cause of reconciliation lies in its ability to reduce uncertainty, alleviating stress. Recently, the hypothesis has been extended (and integrated with the relationship quality hypothesis) following evidence that in Barbary and longtailed macaques both aggressors and victims exhibit increased levels of post-conflict SDB (Aureli in press; Das et al. submitted). Aureli suggests that aggressors and victims alike are uncertain about their opponent's future behaviour because their relationship is at risk and that reconciliation, by repairing the relationship (e.g. de Waal & Yoshihara 1983), also serves to reduce this source of uncertainty.

Other forms of post-conflict behaviour

Redirection of received aggression to a previously uninvolved individual is a well recognised phenomenon among the genus *Macaca*, quantitatively demonstrated among long-tailed (de Waal et al. 1976, Aureli & van Schaik 1991a), Japanese (Aureli et al. 1993) and Barbary macaques (Aureli et al. 1994; see also Scucchi et al. 1988 for a review of qualitative evidence). Redirected aggression has also been reported in vervet monkeys (Cheney & Seyfarth 1986, 1989) and subordinate male and immature mountain gorillas (Watts 1995b). Smuts (1985) attributed redirection to all classes of olive baboons, but an earlier study recorded no instances of redirected aggression by free-ranging adult and subadult male baboons (Eaton 1984). Attacking other members of the group as a response to aggression can attenuate physiological costs and divert attention to other individuals (Aureli & van Schaik 1991b). When targeted upon aggressors'

kin, allies or favoured mates it may impose fitness costs upon opponents (Aureli et al. 1992).

Increased post-conflict affiliation, or *consolation*, between former opponents and non-combatants has been demonstrated formally in chimpanzees (de Waal & van Roosmalen 1979; de Waal & Aureli 1996). However, the absence of a quantitative demonstration of consolation in other species (pigtail macaques: Judge 1991; long-tailed macaques: Aureli & van Schaik 1991a, Aureli 1992; ring-tailed and brown lemurs: Kappeler 1993; Japanese macaques: Aureli et al. 1993; Barbary macaques: Aureli et al. 1994) has led to a proposal that consolation is predicated upon the ability to empathise with the distress of combatants, an aspect of a theory of mind which may be available only to apes (the 'social cognition' hypothesis: de Waal & Aureli 1996). Alternatively, the absence of consolation in macaques may reflect differing social constraints upon non-combatants: among cercopithecines consolation may be too costly to be adaptive because of an increased risk of receiving aggression when attempting to console. A further possibility is that the benefits of consolation are insufficient to prove adaptive (the 'social constraints' hypothesis: de Waal & Aureli 1996).

Other forms of post-conflict affiliation have been reported. *Substitute reconciliation* (Aureli & van Schaik 1991a) where aggressors engage in post-conflict affiliation with the kin of former opponents at increased rates, has been demonstrated in captive pigtail and long-tailed macaques (Judge 1991; Das et al 1996). Captive patas monkeys and free-ranging vervet monkeys also affiliate more frequently with the matrilineal kin of opponents following conflict, although it is unclear whether victims, aggressors or both, exhibited these effects (York & Rowell 1988; Cheney & Seyfarth 1989). The rate of affiliative interaction between pigtail macaque aggressors and their own kin increased following conflict (Judge 1991) while rhesus macaques who had bitten their former opponent then elevated rates of grooming of third parties (*redirected affection*: de Waal & Yoshihara 1983). This class of interactions may reflect efforts to reduce post-conflict tension and/or alternative means of restoring relationships via the affiliative networks of former opponents.

In this thesis I test the relationship quality hypothesis by comparing the post-conflict behaviour of two identically housed captive groups of pigtail macaques with different backgrounds. I then test for the occurrence of reconciliation, consolation and redirection in a wild troop of olive baboons and examine a range of parameters to test their effect on conciliatory behaviour. Finally, I assess the validity of the uncertainty reduction hypothesis in a wild population and explore its applicability to all combatants whatever their role in the initial conflict.

Self-directed behaviour

The self-directed behaviour of primates which includes self-grooming, self-touching, scratching, yawning and body-shaking are forms of 'displacement activity': actions of an animal "apparently irrelevant" to its ongoing activity (Tinbergen 1952; Zeigler 1964). For example, in agonistic or sexual contexts, passerine birds are reported to clean their feathers or bills, eat or drink, or engage in other activities that have no obvious relationship with the primary activity in which they are involved (Morris 1954; Rowell 1961). Analogous behaviour has been described in other taxa including fish and mammals (e.g. Tinbergen & van Iersel 1947; Roper 1984). In all taxa, displacement activities are linked to states of conflict - when two or more incompatible motivational tendencies simultaneously occur - or to situations in which an animal is prevented from achieving its goal (Tinbergen 1952; McFarland 1966).

There is debate over the causes of displacement activity. Tinbergen (1952) hypothesised that tension built up during situations of conflict is released by performing displacement activity. In contrast, van Iersel & Bol (1958) proposed that the inhibition produced by conflicting tendencies allows a third, irrelevant, displacement tendency to gain expression. Finally, Bindra (1959) suggested that animals in conflict or those frustrated from achieving goals experience increased levels of arousal resulting in activities "which are prepotent in the animal's repertoire" prevailing. However, while there is no clear agreement on the mechanism underlying displacement, a group of

Italian ethologists have proposed that "the analysis of the occurrence of displacement activities may provide insight into the emotional state of an animal" (Maestripieri et al. 1992; see also Schino et al. 1988, 1990; Aureli & van Schaik 1991b; Troisi et al. 1991). They reason that attending to displacement activities can provide a degree of access to the emotional state of the study animal because the expression of displacement activities is associated with a state of internal conflict and because conditions of motivational ambivalence are thought to have an emotional dimension in the form of anxiety or uncertainty. Indeed, experimentally induced conflict situations produce physiological autonomic responses including respiratory and circulatory changes (e.g. Andrew 1956b) and such physiological changes produce a set of stimuli arising from the pelage, skin and blood vessels which could be expected to elicit a range of self-maintenance activities (Andrew 1956a, b).

A number of studies of non-human primates support the suggestion that displacement activities could provide insight into the emotional state of the subjects. First, there are several anecdotal reports of SDB occurring in situations where behavioural ambivalence and anxiety might be expected. For example, Smuts (1985) describes a female olive baboon who "scratched herself several times, as baboons often do before making a decision" over whom to feed near. Hadidan (1980) and Bertrand (1969) report similar behaviour in crested and stumptail macaques, while Kummer (1968; 1995) comments upon high rates of scratching among male hamadryas baboons, *P. hamadryas*, during the initiation of group movements.

In a more formal study, Diezinger & Anderson (1986) interpret increased scratching rates in captive rhesus macaques around the time of changes in behaviour in terms of behavioural indecision. Maestripieri (1993) reported that rhesus mothers scratched more frequently both when their infants moved away from them, and when their infants came into proximity with individuals who habitually harassed them. In long-tailed macaques, the self-grooming and scratching rates of females were at their highest when they were within 1 m of the alpha male (Troisi & Schino 1987; Pavani et al. 1991), and the delayed establishment of dominance relationships between

unfamiliar female pairs resulted in marked increases in scratching, self-grooming and yawning (Schino et al. 1990). As discussed above, several studies have reported increases in the SDB rate of victims following aggression and reductions when former opponents reconcile (Aureli et al 1989; Aureli & van Schaik 1991b; Aureli in press; Das et al. submitted; de Waal & Aureli in press) and there is independent physiological evidence of increased heart rate in the post-conflict period and its attenuation by affiliation (Boccia et al. 1989; Smucny et al. 1996). Finally, since anxiogenic drugs increase and anxiolytic drugs reduce SDB expression, pharmacological evidence also supports the link between SDB and anxiety (Ninan et al. 1982; Insel et al. 1984; Schino et al. 1991).

In this thesis, I investigate the viability of SBD as an index of stress in a wild population of olive baboons by examining SDB response following aggression and post-conflict affiliation. I then examine the expression of SDB outside situations of physical conflict. Principally, I test the effect of near neighbour dominance status on the frequency with which sexually mature female baboons engage in SDB and assess the potential of this measure as an index of relationship security.

Outline of thesis

Chapter 2 details a study of two large groups of pigtailed macaques living in identical outdoor enclosures at the Yerkes Primate Center, Georgia, USA. I examine and compare their conciliatory behaviour in the context of other aspects of their social behaviour and the relationship quality hypothesis. In Chapter 3, I present a brief overview of the olive baboons and the study site on which I concentrate for the remainder of the thesis. Chapter 4 and Chapter 5 examine the post-conflict behaviour of this population. In Chapter 4, I test whether wild olive baboons show conciliatory patterns characteristic of captive cercopithecines and examine a range of factors thought to be predictive of conciliatory behaviour. I also test whether individuals in this population became involved in elevated rates of affiliation with supporters and individuals uninvolved in the original conflict, and whether victims

redirect aggression to third parties in the immediate post-conflict period. Having established that wild baboons do indeed reconcile some of their conflicts, Chapter 5 presents a test of the uncertainty reduction hypothesis and establishes that self-directed behaviour is indicative of post-conflict stress in this population. In Chapter 6, I explore the nature of SDB outside aggressive contexts, testing whether the dominance status of neighbouring baboons affects SDB expression and considering the utility of a measure of SDB expression relative to time spent in proximity as an index of relationship security. Finally, Chapter 7 presents a concluding discussion of the results presented in this thesis.

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Chapter 2. VARIATION IN CONCILIATORY TENDENCY AND RELATIONSHIP QUALITY ACROSS GROUPS OF PIGTAIL MACAQUES

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Abstract

Previous studies suggest that the tendency for primates to reconcile after agonistic conflict is related to the quality of relationships between opponents: the 'relationship quality' hypothesis. In addition, reconciliation frequency seems to covary with other social variables such as the rate of allogrooming, the intensity of aggression, and the outcome of approaches: the 'systematic variation' hypothesis. It is proposed that such 'systematic variation' should be present not only between different species but also between different groups of the same species. To test these hypotheses, data were collected from two large corral-housed groups of pigtail macaques, *Macaca nemestrina*, over seven months. The two groups lived in identical environments but one was well-established, the other newly formed. In both groups, conflicts were more frequently reconciled between opponents with strong affiliative ties, as predicted by the relationship quality hypothesis. Members of the well-established group reconciled roughly twice as often as members of the newly formed group. Contrary to the predictions of the systematic variation hypothesis, other social variables did not vary between groups. Members of the well-established group, however,

distributed their affiliative behaviour less evenly, focusing their efforts on a relatively small number of partners. The concentrated social networks in the well-established group apparently produced more intense ties, hence increasing the likelihood of reconciliation after conflict. These results show that detailed analyses of social networks provide a tool to investigate the systematic variation hypothesis when variation is subtle, such as between groups of the same species. Our study confirms the relationship quality hypothesis at both the within- and between-group level, provides support for a more sophisticated conception of systematic variation, and illustrates the special usefulness of reconciliation measures as a gauge of social integration.

Introduction

Within-group competition is constrained by its negative consequences, which range from the risk of injury to potential damage to social relationships (de Waal 1989a). One way to cope with these negative effects is to repair relationships after conflict. Friendly interactions between former opponents following aggression have been observed in a number of non-primate species (e.g. mouflon, *Ovis ammon*: Pfeffer 1967; spotted hyena, *Crocuta crocuta*: Kruuk 1972; lion, *Panthera leo*: Schaller 1972; dwarf mongoose, *Helogale undulata*: Rasa 1977; feral ram, *Ovis aries*: Rowell & Rowell 1993), and quantitatively demonstrated in a variety of primate species (reviewed by de Waal 1989b, 1993; Kappeler & van Schaik 1992). In support of the postulated function of social repair, post-conflict reunions between former opponents, or 'reconciliations' (de Waal & van Roosmalen 1979), have been found to 1) reduce the likelihood of further aggression (Aureli & van Schaik 1991b; Cords 1992; de Waal 1993), 2) lower the frequency of behavioural indicators of anxiety (Aureli et al. 1989; Aureli & van Schaik 1991b), and 3) restore tolerance within relationships (Cords 1992).

The frequency of reconciliation depends on the quality of relationships between opponents, especially their value (i.e. the 'relationship quality' hypothesis: de Waal & Yoshihara 1983; Aureli et al. 1989; Kappeler

& van Schaik 1992). For example, affiliative interactions in long-tailed macaques, *Macaca fascicularis*, increased dramatically following conflict between partners that had learned to collaborate to get food (Cords & Thurnheer 1993). Furthermore, in species with highly co-operative matrilineal kin relationships, such as some macaques, related individuals tend to reconcile more often than unrelated ones (Aureli et al. 1989, 1997; Thierry 1990b; Judge 1991; Call et al. 1996; cf. Thierry 1990a). In chimpanzees, *Pan troglodytes*, where males form alliances with one another that serve both within- and between-group competition, and females have relatively loose relationships, conflicts between males are more often reconciled than those between females (Goodall 1986; de Waal 1986; but see Baker & Smuts 1994), while in mountain gorillas *Gorilla gorilla beringei*, where males are important to females both as social partners and as protectors, conflicts between females and adult males are reconciled but not conflicts with immatures or other females (Watts 1995a).

The value of relationships may also explain interspecific differences in reconciliation frequency. For example, in species that engage in intensive between-group competition, each group member is highly valuable for co-operative efforts against other groups and so reconciliation frequency with the average group member is expected to be high (de Waal 1989b; de Waal & Luttrell 1989). Interspecific comparisons provide, therefore, an opportunity to investigate the relation of the tendency to reconcile with other aspects of social organisation. Even closely related species sometimes differ on dimensions such as group cohesiveness, strictness of the dominance hierarchy, social tolerance, and rates of affiliative behaviour. For example, stumptail macaques, *M. arctoides*, groom more than rhesus monkeys, *M. mulatta*, are less intensely aggressive, have more symmetrical contests, approach one another more often and with fewer negative results (de Waal & Luttrell 1989), and also reconcile a greater proportion of their conflicts (de Waal & Ren 1988).

Thierry (1987, 1990b) also stressed the co-variance of behaviour in his studies of three macaque species. Paralleling de Waal and co-workers' comparison of rhesus and stumptail macaque dominance styles, Thierry

noted that species with more intense aggression, the rhesus and long-tailed macaques, have also more unidirectional contests, less frequent reconciliation and fewer affiliative interactions outside the context of aggression. In contrast, the low intensity of Tonkean macaque, *M. tonkena*, aggression is associated with bi-directional contests, frequent conciliatory behaviour and high affiliation (Thierry 1984, 1985, 1986).

Different dimensions of social organisation may vary together either as a co-evolved set in response to selective ecological pressures, or as a complex of adaptive traits to a particular current environment, including captivity. Vehrencamp (1983) and van Schaik (1989) propose that such variation forms a continuum ranging from the relative co-operation of 'egalitarianism' to the intolerance of 'despotism'. Both authors emphasised the importance of the subordinates' options outside the group (for example, the possibility and risk of transfer to another group) in determining the level of tolerance of dominant individuals towards lower-ranking conspecifics.

The Tonkean macaque society is classified as egalitarian and tolerant because interactions between group members are relatively benign, while rhesus society earns the label of despotism through the negative nature of within-group interactions. We propose that if such patterns of co-adaptation are typical of primate groups, there should exist systematic variation of behavioural traits from group to group and from species to species. According to this 'systematic variation' hypothesis (implicit in the work of Thierry and de Waal), individuals of a group (or species) that differ in one trait from individuals of another group (or species), should show similar variation in the remaining co-adapted traits. That is, all measures of social tolerance should vary together: a tolerant/egalitarian species (or group) should show relatively high conciliatory tendency alongside more frequent approaches. A greater proportion of those approaches should be made by subordinate individuals and they should have fewer negative resolutions. In addition, other measures of affiliation, such as allogrooming should be elevated and aggression should be less intense (lower rates of attack and biting) and more often bi-directional.

The 'relationship quality' and the 'systematic variation' hypotheses are not alternative, rather they complement each other. Systematic variation is based upon the principle that an individual will vary its behaviour towards a conspecific according to the benefits that can be derived from their relationship, that is, the value of their relationship. Systematic variation at the group-level exists because the quality of relationships varies across groups and species; it reflects fluctuations in the quality of relationships such that a group or species in which the average group member is highly valuable will systematically engage in tolerant social interactions. By contrast, in groups or species in which relationships are on average of lower quality, behaviour toward other group members will be relatively despotic.

The purpose of our study was twofold. Our first aim was to test the relationship quality hypothesis by examining the association between reconciliation frequency and relationship quality within and between two captive groups of pigtail macaques. These groups lived under identical environmental conditions, yet had quite different backgrounds: one was well-established; the other newly formed. We predicted that within either group, dyads exhibiting high conciliatory tendency should be characterised by comparatively high levels of affiliation. Furthermore, any between-group difference in reconciliation frequency should be associated with a between-group difference in average relationship quality.

Our second aim was to test the systematic variation hypothesis through further comparisons of the social behaviour of the two groups. This hypothesis predicts that higher conciliatory tendency in one group (as evidence of higher average relationship quality within that group) should be accompanied by further indicators of a tolerant dominance style.

Methods

Subjects

We studied two groups of pigtail macaques living in virtually identical 30.5 by 30.5 m outdoor enclosures with attached indoor quarters (9.2 x 3.0 x 2.0 m) at the Yerkes Regional Primate Research Center Field Station,

Lawrenceville, Georgia, USA. The enclosures had gravel floors and contain concrete culverts and steel scaffolds connected by climbing material. The animals were fed monkey chow twice daily, fruit or vegetables once daily and had ad libitum access to water.

The two groups differed considerably in demography. All monkeys of the 'Old' group were born at the Field Station. The group, formed in 1963, had been subject to occasional removals and additions for management purposes. Details of the group's formation and activity patterns are available in Bernstein (1969, 1972). During the study, group size ranged from 48 to 53 individuals, including two adult males (at least 7 years of age at the beginning of the study), 27 adult females (at least 3.5 years old), two juvenile males (between 1.5 and 5 years), five juvenile females (between 1.5 and 3.5 years), and 21 individuals younger than 1.5 years. There existed five matrilineal kinship units, ranging in size from two to nine adults per unit. During the course of the study one adult male and three adult females either died or were permanently removed owing to poor health.

The 'New' group was established in June 1991, just 1.5 years prior to our study which started in December 1992. Total group size ranged from 59 to 65 individuals including five adult males (originally members of Old group), one sub-adult male (between 5 and 7 years), 32 wild-born adult females, and 30 individuals younger than 1.5 years. At the outset of our study there were no juveniles in the group and all females were between 5 and 7 years of age (estimates based on weight and dental condition). The exact origins of the females are not known but the restricted age structure suggests few kin relations within this group.

Procedure

During data collection the monkeys were locked in the outdoor compounds. D. L. C. collected all the data, using several sampling techniques.

Standard focal observations

Focal observations (Altmann 1974) were made of aggression, approaches and approach outcome as spoken accounts on a cassette recorder. We collected 4 h of focal observations (i.e. 16 samples of 15 min each) on each of 15 (five male, 10 female) adult subjects in New group and 14 (one male, 13 female) adult subjects in Old group. An adult male from Old group was the subject of 5 observations before his removal from the group. All adult males present in the groups were focal subjects. We selected female subjects with regard to age, matrilineal membership (Old group only) and rank to ensure a representative sample. We collected this type of data from 4 December 1992 until 25 May 1993. For each subject, observations were equally divided over the study period as well as over the time of day, between 0900 and 1700 hours.

Scan samples

We employed an instantaneous scan sampling procedure (Altmann 1974) to study associative-'state' behaviour. At 15 min intervals the group was scanned from left to right and all instances of allogrooming, sitting in contact or proximity (within 0.5 m), and play were recorded. If a major agonistic incident occurred during a sample, the sample was cancelled. Scan data for both groups covered the same period as the focal observations. The data set consists of 275 scan samples on Old group and 267 scan samples on New group. Observations were equally divided over the study period and over the time of day between 0900 and 1700 hours.

Post-conflict observations

We collected data on reconciliation behaviour from 4 December 1992 until 29 June 1993. The method was based on de Waal & Yoshihara's (1983) study and consisted of a post-conflict focal observation (PC) of 10 min on an individual involved in an agonistic incident of sufficient intensity (minimally including a chase of over 2 m or biting). PCs started immediately after the last agonistic behaviour pattern was observed, unless the conflict flared up again within 2 min. For each aggressive interaction we recorded the identity of the recipient(s) and of the aggressor(s), the intensity of the

attack, and the outcome of the conflict (focal wins, loses, or draws). A drawn conflict was defined as one in which the recipient of aggression countered with aggression and neither opponent showed clear signs of submission.

For each PC one participant was selected as the focal subject, the 30 individuals chosen for standard focal observations (described above) having priority over all others. In addition, rarely sampled individuals were favoured and adult individuals were preferred to younger animals. Finally, subjects were selected to produce a balance between recipients and initiators of aggression.

During the PC we recorded all agonistic and affiliative interactions in which the focal individual was involved. For each interaction we also recorded the identity of the partner and the initiator (e.g. who approached). Affiliative interactions included 'allogrooming', 'sitting in contact', 'embracing', 'playing', 'muzzle contact', 'exchange of lipsmacking', and various forms of 'touching' and 'mounting'.

Each PC was compared with a matched-control observation (MC), collected on the next possible observation day, matched to the PC with respect to duration, focal subject, and starting time. If the focal subject was involved in aggression just before, or within the first two minutes of, the MC, the observation was postponed until the next possible day. This PC-MC method was followed 156 times for Old group and 198 times for New group. In some PCs the focal subject had more than one opponent, so that this method produced data on a total of 174 and 223 PC-MC opponent-pairs, in Old and New group, respectively.

Other agonistic records

The inter-individual direction of the 'silent bared-teeth face' (van Hooff 1967) and 'fierce biting' (de Waal & Luttrell 1989) was recorded whenever observed (all occurrences sampling; Altmann 1974). We collected data from 4 December 1992 until 29 June 1993. The number of all occurrences observation hours was 247 for Old group and 249 for New group.

Ad libitum observations of dyadic agonistic behaviour and silent bared-teeth face collected during the same period by D. Maestripieri, T.

McCaster and the D. L. C. were added to the data set for the construction of a dominance hierarchy.

Analysis

To examine the existence of social events characteristic of post-conflict situations we used both the method developed by Aureli et al. (1989) and Aureli & van Schaik (1991a), which we refer to as the 'time rule', and that described by de Waal & Yoshihara (1983), which we refer to as the 'PC-MC method'. According to the PC-MC method, a pair of former opponents is said to be 'attracted' if they engage in affiliative interaction during the PC only, or earlier during the PC than during the MC. The pair is said to be 'dispersed' if such interaction occurs in the MC only, or earlier during the MC than in the PC.

We employed Veenema et al.'s (1994) revised measure of Conciliatory Tendency (a measure of reconciliation frequency that fully controls for baseline levels of affiliation). For any focal individual let *a* be the number of attracted pairs; let *d* be the number of dispersed pairs; and let *t* be the total number of PC-MC pairs for that individual. Then conciliatory tendency = $(a - d) / t$. Conciliatory tendency is measured per focal individual regardless of whether it was this individual or its opponent that initiated the interaction.

Other behavioural measures used are identical to de Waal & Luttrell (1989):

Grooming duration: performed allogrooming as a percentage of 15 min instantaneous scan samples.

Approach frequency: the number of non-agonistic approaches to within 0.5 m of another individual per h of focal observation.

Negative approach result: the percentage of non-agonistic approaches during focal samples with a socially negative outcome (i.e. teeth-baring, pushing, grabbing, approachee withdraws from or threatens approacher).

Up/down approach direction: the tendency to approach dominant versus subordinate individuals during focal samples is expressed in a 'up-down index'. Let u be the number of approaches made by an individual to higher-ranking adults divided by the number of such adults. Let d be the same individual's number of approaches to lower-ranking adults divided by the number of such adults. The up/down index = $u / (u + d)$. The index will be 0.5 if relative rank has no influence on approach direction. A higher index indicates a bias towards approaching dominants, a lower index a bias towards approaching subordinates.

Threat frequency: the number of initiated aggressive acts per h of focal observation not exceeding the threat intensity. Threat is defined as staring open-mouth facial expressions often accompanied by rough, low-pitched vocalisations (de Waal et al. 1976). The category also includes lunges of less than 2 m.

Attack frequency: the number of initiated aggressive acts per h of focal observation exceeding the threat intensity, including chases of over 2 m, biting, and fierce biting (i.e. biting sustained for more than 5 s, and/or accompanied by head shaking, and/or resulting in injury).

Fierce biting frequency: the number of fierce bites per 100 h of observation collected with the all occurrences sampling technique.

Counter aggression: the percentage of initiated aggressive acts during focal observations to which the recipient responded with aggressive behaviour of any intensity.

These behavioural measures concern adults only. Partners and opponents could be immature, but behaviour directed towards individuals younger than 1.5 years was ignored (see de Waal & Luttrell 1989). Approach data concern adult-adult dyads only. Individual means and standard deviations are provided per group ('Overall' measure). As group demography differed, we calculated two other types of measure. To eliminate the possibility that a between-group difference in the number of adult males could affect the results, the analyses were further limited to the interactions of adult females with other adult females ('Adult females' measure). As a control for group size, behavioural frequencies were divided

by the number of potential partners in each group for both the 'Overall' and 'Adult females' measures.

Kinship refers to matrilineal relationships, regardless of genetic distance and paternity. We determined dominance hierarchies on the basis of the inter-individual direction of silent bared-teeth face and the outcome of dyadic agonistic interactions.

We used a diversity index to compare affiliative distribution between groups. This index is a measure of the extent to which adults affiliate evenly with other group members. Using scan sample data of grooming (performed and received), sitting in contact or in proximity (within 0.5 m), and play we derived a measure of adults' affiliation with each group member: the number of scans in which two individuals affiliated as a proportion of scans in which they were present together in the group. This measure was summed for all possible partners of each adult and the amount of affiliation devoted to each partner as a proportion of this sum was calculated. These values were used to calculate Shannon's heterogeneity index for each adult: $H = -\Sigma p_i \ln p_i$, where p_i is the proportion of scan samples in which each adult affiliated with the individual *i*. Then Buzas and Gibson's (1969) evenness index was applied to compensate for group size: $H^* = \exp(H) / n$, where n is the number of available partners. We compared the values of H^* for each individual across groups to examine between-group differences in the social networks (H^* has a range from 0, where the individual affiliates with just one other animal, to 1, where affiliation is evenly distributed among all other group members).

We carried out two-tailed non-parametric statistical tests at the individual level, except when otherwise stated. Mann-Whitney *U*- and Wilcoxon matched-pairs tests included corrections for ties. Where samples sizes were too small for analysis at the level of the individual, we used Chi-squared analyses of pooled data. These are interpreted as descriptive and with caution.

Results

Reconciliation

The demonstration of reconciliation

According to the 'time-rule' we determined for each PC and MC observation in which minute the first affiliative interaction between former opponents was made. Former opponents in both groups had a higher tendency towards affiliative interaction soon after the end of the agonistic conflict than in control periods (Fig 1). Kolmogorov-Smirnov tests showed that the PC and MC distributions were significantly different (Old group: $D=0.841$, $p<0.001$; New group: $D=0.834$, $p<0.001$; in both groups the greatest difference in the cumulative distributions was within the first 2 min). These data are based on dyadic conflicts; for polyadic conflicts PC curves closely resembled those for dyadic conflicts. These results demonstrate that former opponents contacted each other sooner in the PCs than MCs.

This was confirmed at the individual level as most focal individuals were involved in affiliation with former opponents more often in the first 2 min of PCs than in the first 2 min of MCs (Wilcoxon matched-pairs test; Old group: $N=23$, $z=3.92$, $p<0.001$; New group: $N=34$, $z=4.33$, $p<0.001$). These results were also confirmed using the PC-MC method. In both groups the proportion of attracted pairs per focal subject was higher than the proportion of dispersed pairs (Old group: 42.8% attracted, 0.9% dispersed; $N=23$, $z=3.91$, $p<0.001$. New group: 26.8% attracted, 6.4% dispersed; $N=34$, $z=3.81$, $p<0.001$).

Selective attraction

It could be argued that the increase in affiliative interactions between former opponents after a conflict is the result of a general increase in the tendency of individuals involved in agonistic conflicts to act affiliatively rather than the result of a specific attraction between the two opponents. This possibility was tested by comparing the identity of the partners with which the focal animal had affiliative interactions in the PCs with that in the MCs. We counted the number of different individuals contacted in the course of an observation period, regardless of initiative to contact. Next, the number of

Figure 1

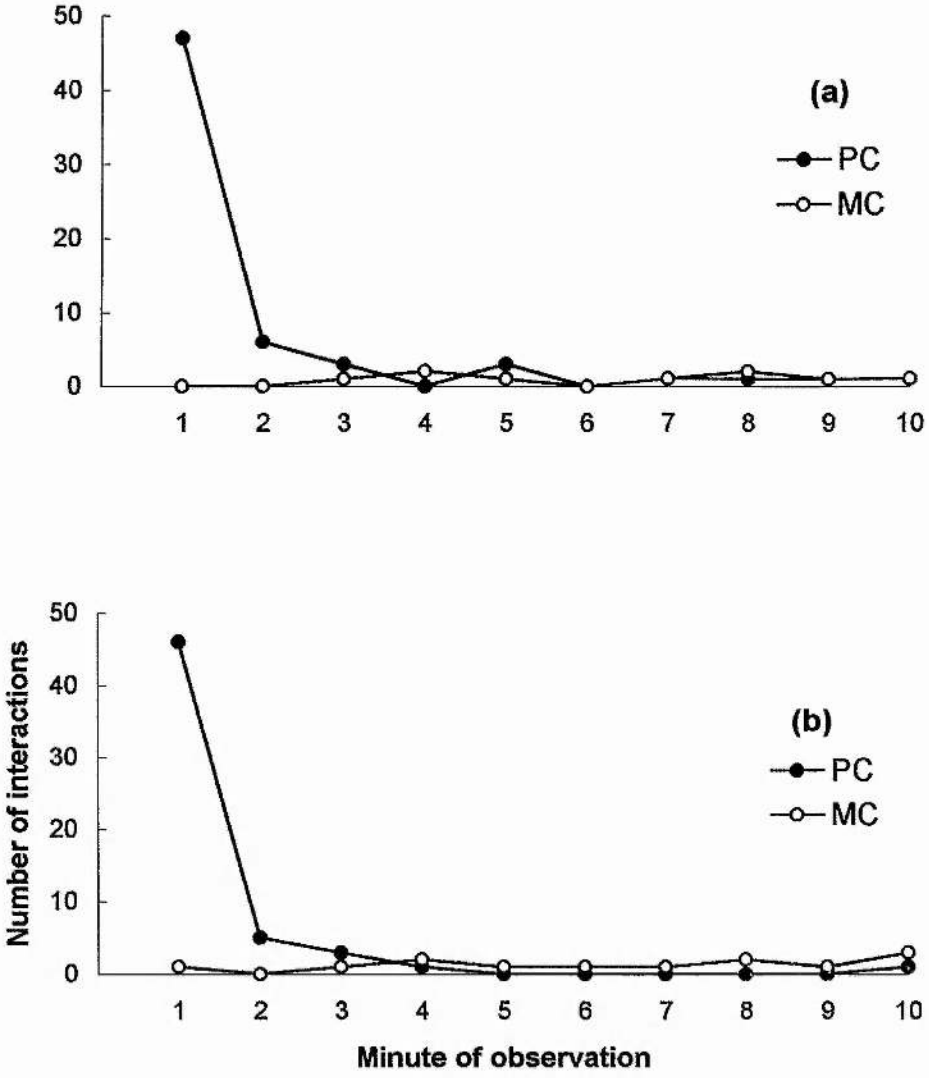

Figure 1. Distribution of the first affiliative interaction between former opponents during the 10 min post-conflict (PC) and matched-control (MC) observations in (a) Old and (b) New groups.

former opponents contacted was expressed as a percentage of the number of contact partners (see de Waal & Yoshihara 1983). For Old group, former opponents were the partners in 18.1% of these contacts during the PCs and only 3.5% during the MCs (N=22, z=3.82, p<0.001). In New group former opponents were the partners in 15.1% of the affiliative interactions during the PCs and 6.8% during the MCs (N=33, z=3.88, p<0.001). We can therefore conclude that the attraction between former opponents after a conflict was selective.

Initiative

We tested whether recipients of aggression were more likely than aggressors to take the initiative to reconcile. The analysis was limited to conflicts in which the direction of aggressive behaviour was unambiguous (i.e. excluding incidents with mutual aggression). First, we calculated the proportion of approaches made by recipients of aggression leading to the first affiliative interaction between former opponents in PCs. We compared this figure to the proportion of such approaches leading to affiliative interaction in the corresponding MCs. Owing to small sample sizes in the MCs, we could not examine the difference between the two proportions at the individual level. Testing pooled data did not reveal any difference for Old group: 33% of 67 first PC interactions were initiated by the recipient of aggression versus 35% of 23 interactions in the MCs (χ^2=0.007, df=1, NS; adult females: 33% of 48 versus 42% of 19: χ^2=0.15, df=1, NS). In contrast, New group recipients of aggression were more likely to initiate reconciliation than aggressors (50% of 60 first PC interactions versus 24% of 21 interactions in the MCs: χ^2=5.48, df=1, p<0.05; adult females: 48% of 48 versus 22% of 18: χ^2=4.72, df=1, p<0.05).

Specific affiliative acts

In the two groups combined, we recorded only one instance of both 'mutual lipsmacking' and 'play'. Therefore, we excluded these behaviour patterns from the comparison of PC and MC distributions. There was no

difference in the distribution of specific acts in New group (χ^2=3.05, df=5, NS; adult females: χ^2=3.39, df=5, NS), whereas we found a significant difference for Old group (χ^2=14.38, df=5, $p<0.05$; adult females: χ^2=11.58, df=5, $p<0.05$) mainly owing to a high proportion of 'mounting' during PCs (χ^2=5.72, df=1, $p<0.05$; adult females: χ^2=3.78, df=1, p=0.052; Fig 2). Most of the cases (13 out of 18 'mounts', i.e. 19% of all PC specific acts; adult females: 8 of 11, 17%) in this category were not complete mounts but consisted of a so-called 'standing grasp' in which one individual crouched over the hindquarters of the partner from behind with or without foot-clasping.

Between-group Comparisons

Reconciliation and other behavioural measures

We compared the reconciliation frequencies of the two groups after calculating the conciliatory tendency of each adult individual that was sampled as a focal subject with the PC-MC method. Old group's mean conciliatory tendency was twice that of New group for both the overall and adult female measure (Table I).

None of the other behavioural measures showed significant differences between the two groups for either the overall or the adult female measure (Table I). Comparisons of behavioural measures divided by number of potential partners (Table II) also produced no significant difference.

Social networks

All measures presented in Table I are average individual behavioural scores with other group members. As such, these measures fail to use most of the variance in the original data; for example, they indicate the amount of time pigtail macaques devote to allogrooming but they dispense with information on how the grooming was distributed among the available partners. It is possible that the two groups differed in the number of affiliative partners animals interacted with. If this is the case then, the systematic

Figure 2

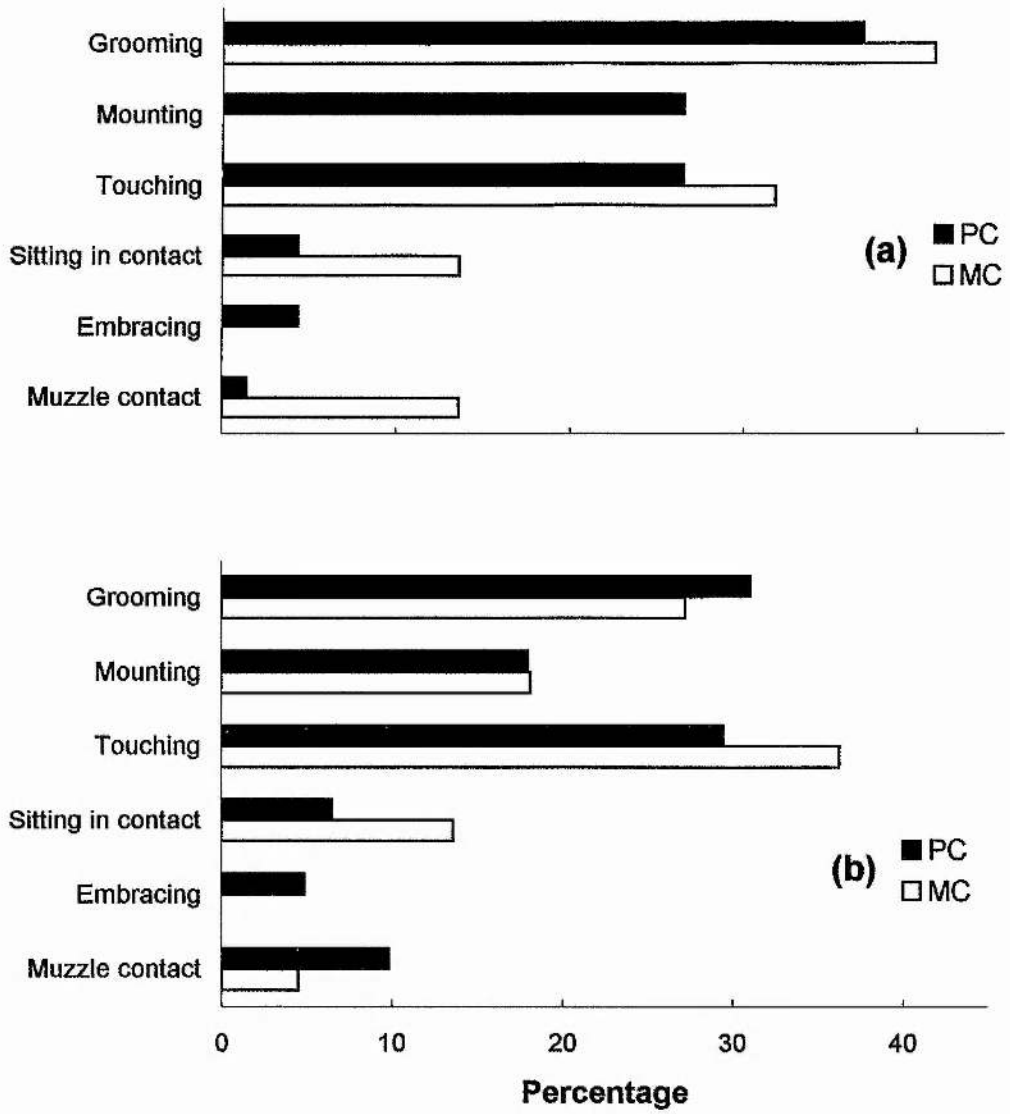

Figure 2. The occurrence of six affiliative acts during the first post-conflict (PC) interaction between former opponents and during all matched-control (MC) observations for the same dyads of former opponents in (a) Old group and (b) New groups. The percentage is the expression of the relative frequency of each affiliative act.

Table I. Nine behavioural measures on Old and New groups.

	Old group		New group			
Overall	N	mean ± SD	N	mean ± SD	*U*	P
Conciliatory tendency (%)	23	41.9 ± 27.0	34	20.4 ± 30.0	2.76↑	**
Grooming duration (%)	26	7.6 ± 4.8	36	7.4 ± 3.7	0.17↑	NS
Approach frequency / h	15	22.23 ± 9.31	15	26.85 ± 17.15	105.0	NS
Negative approach (%)	15	13.2 ± 4.8	15	10.6 ± 7.0	77.5	NS
Up / down direction	14	0.35 ± 0.19	14	0.33 ± 0.24	90.0	NS
Threat frequency / h	15	0.50 ± 0.74	15	0.32 ± 0.50	88.0	NS
Attack frequency / h	15	0.22 ± 0.23	15	0.28 ± 0.46	108.5	NS
Fierce biting / 100 h	26	0.95 ± 1.39	36	1.66 ± 2.21	0.84↑	NS
Counter-aggression (%)	12	6.2 ± 15.5	10	1.0 ± 3.2	55.0	NS
Adult females						
Conciliatory tendency (%)	20	41.6 ± 27.8	29	22.6 ± 32.6	2.40↑	*
Grooming duration (%)	24	6.0 ± 4.4	31	5.4 ± 2.7	0.91↑	NS
Approach frequency / h	13	20.83 ± 9.70	10	21.20 ± 12.09	64.5	NS
Negative approach (%)	13	13.4 ± 5.6	10	8.4 ± 5.2	34.5	NS
Up / down direction	12	0.28 ± 0.19	10	0.45 ± 0.25	36.0	NS
Threat frequency / h	13	0.14 ± 0.24	10	0.08 ± 0.12	61.5	NS
Attack frequency / h	13	0.14 ± 0.16	10	0.12 ± 0.18	62.0	NS
Fierce biting / 100 h	24	0.78 ± 1.09	31	1.83 ± 2.25	1.16↑	NS
Counter-aggression (%)	10	0.0	6	0.0		

The table provides the number of adult subjects on which the measure is based (N), individual means and standard deviations (SD). The conciliatory tendency is calculated following the correction in Veenema et al. (1994) and, therefore, is different from that in Table I in de Waal & Luttrell (1989). For the Overall category, the three approach measures (approach frequency, negative approach result and up/down direction) concern adult-adult interactions only; all other measures concern behaviour towards individuals of at least 1.5 years of age. The Adult female category provides measures for interactions between adult females only. The table also provides the outcome (*U*) of Mann-Whitney *U* tests comparing Old group to New group (↑ identifies the cases in which *z* values were used because of larger sample sizes).

**P<0.01, *P<0.05, two-tailed.

Table II. Five behavioural measures controlled for group size on Old and New groups.

	Old group		New group			
Overall divided by available partners	N	mean ± SD	N	mean ± SD	*U*	P
Grooming duration (%)	26	0.24 ± 0.15	36	0.21 ± 0.10	0.61↑	NS
Approach frequency / h	15	0.92 ± 0.38	15	0.78 ± 0.50	92.0	NS
Threat frequency / h	15	0.016 ± 0.024	15	0.009 ± 0.014	82.5	NS
Attack frequency / h	15	0.007 ± 0.007	15	0.008 ± 0.013	92.0	NS
Fierce biting / 100 h	26	0.03 ± 0.04	36	0.05 ± 0.06	0.40↑	NS
Adult females divided by available partners						
Grooming duration (%)	24	0.26 ± 0.19	31	0.18 ± 0.09	1.46↑	NS
Approach frequency / h	13	0.91 ± 0.42	10	0.72 ± 0.41	47.0	NS
Threat frequency / h	13	0.006 ± 0.011	10	0.003 ± 0.004	58.5	NS
Attack frequency / h	13	0.006 ± 0.007	10	0.004 ± 0.006	54.0	NS
Fierce biting / 100 h	24	0.03 ± 0.05	31	0.06 ± 0.08	0.90↑	NS

See footnote to Table I for explanations.

variation hypothesis would predict that Old group's higher reconciliation rate should be associated with a more egalitarian affiliative distribution.

We examined each individual's affiliative distribution by means of Shannon's heterogeneity index corrected for group size (i.e. Buzas & Gibson's H^*). We calculated individual affiliative scores by summing scan sample data of grooming (performed and received), sitting in contact or in close proximity (within 0.5 m), and play with each group member. Then, we compared the values of H^* for each individual across groups. Contrary to the expected relative egalitarianism of Old group, New group monkeys distributed their affiliation more evenly than monkeys of Old group (Old group H^*=0.501, New group H^*=0.655; Mann-Whitney U-test: N_1=26, N_2=36, z=3.82, p<0.001). This effect was also evident for affiliation between adult females (Old H^*=0.53, New H^*=0.691; N_1=24, N_2=31, z=3.88, p<0.001). Pigtail macaques of Old group affiliated more with their first and second favoured partners (Fig 3): in Old group, individuals affiliated with their two most favoured partners in 32% of scans, on average; New group individuals affiliated in only 17.2% of scans (N_1=26, N_2=36, z=3.31, p<0.001; adult females: Old 26%, New 17.8%; N_1=24, N_2=31, z=2.02, p<0.05). Monkeys in New group affiliated with significantly more group members than did monkeys in Old group (mean number of partners; Old 28.7, New 32.2; N_1=26, N_2=36, z=5.08, p<0.001; adult females: Old 21.0, New 28.2; N_1=24, N_2=31, z=6.44, p<0.001). These differences were still significant when the number of partners was divided by the number of available individuals in each group (N_1=26, N_2=36, z=2.11, p<0.05; adult females: N_1=24, N_2=31, z=3.32, p<0.001). Thus, affiliative relationships in Old group appeared more selective and also more intense because the two groups affiliated at similar rates. Indeed, if any difference between the groups could be detected in rate of affiliation, it was a trend towards more affiliation between New group females (mean percentage of scans with affiliation: Old 76.3%, New 71.3%; N_1=26, N_2=36, z=0.41, NS; adult Females: Old 58.3%, New 66.2%; N_1=24, N_2=31, z=1.82, NS).

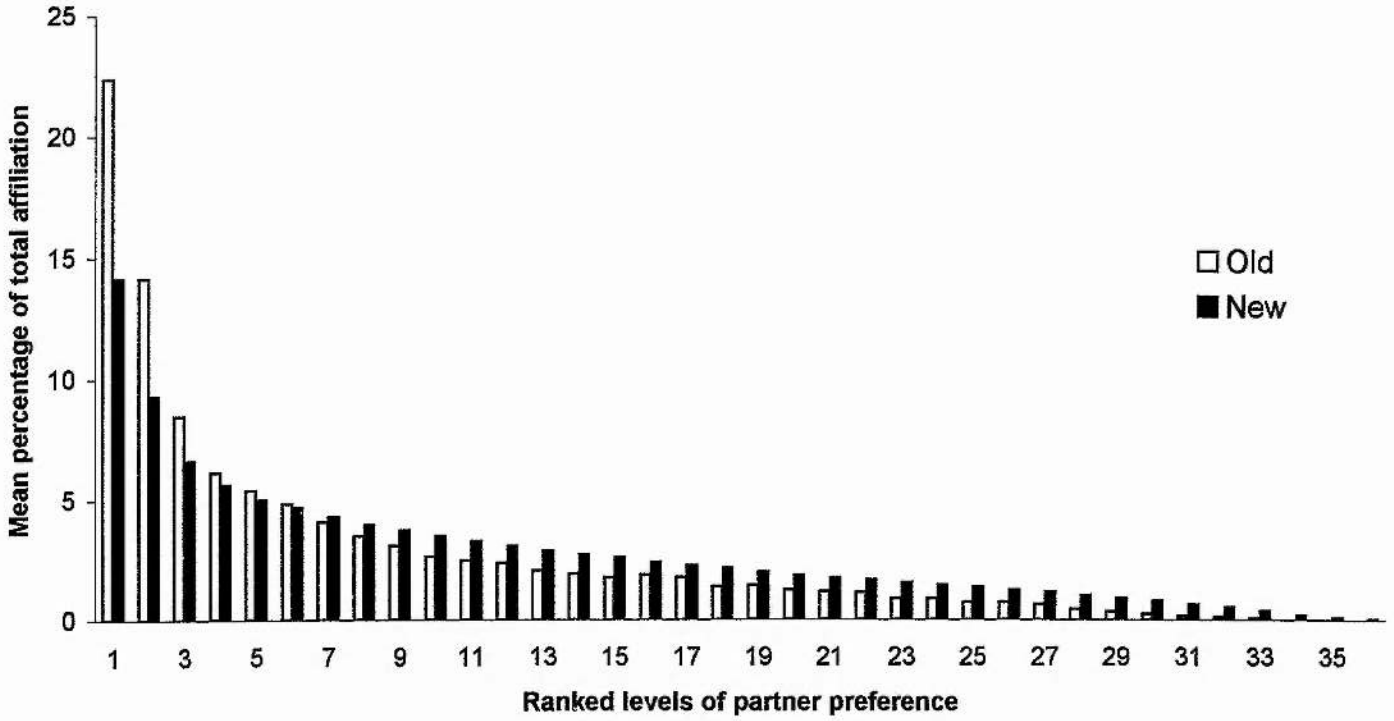

Figure 3. Mean percentage of total affiliation between partners in Old and New groups. Most favoured affiliates are identified by lower numbers.

Figure 3

Reconciliation and relationship quality

Given that Old group's social network is more selective, we decided to investigate the effect of two aspects of relationship quality on conciliatory tendency, namely kinship and level of affiliation. For individuals involved in conflicts with both kin and non-kin we compared the frequency of reconciliation for these two opponent categories. Such analysis could be completed only for Old group because of the small number of known kin relations in New group. In a significant majority of focal subjects the Conciliatory Tendency was higher with related opponents (mean=62.7%, N=19) than with unrelated opponents (mean=37.2%, N=22; permutation test for paired replicates: N=18, 6,268 sums $\geq$ observed sum, $p<0.05$). Adult female scores showed the same pattern (kin 60.0%, non-kin 32.0%; pooled data) and, when we included juvenile females to increase the sample size, the inter-group difference was confirmed (kin mean=64.8%, N=18, non-kin mean=35.6%, N=20; permutation test: N=17, 5,124 sums $\geq$ observed sum, $p<0.05$). Thus, the effect of kinship may explain some of the between-group difference in reconciliation frequency: kin reconciled more often than non-kin and in New group there were fewer related adults than in Old group.

However, in only 42 of the 174 Old group PC-MC pairs were opponents related (25 of 122 adult female pairs) and the Conciliatory Tendency between non-kin in Old group (37.2%) tended to be higher than the overall conciliatory tendency of New group (20.4%; one-tailed Mann-Whitney *U*-test: $N_1=22$, $N_2=34$, $z=1.72$, $p<0.05$; adult females: Old 36.0%, New 22.6%: $N_1=19$, $N_2=29$, $z=1.32$, $p=0.09$). Consequently, kinship cannot fully account for the observed between-group difference in reconciliation frequency.

We categorised an individual's social relationships by expressing the amount of affiliation devoted to a given partner as a percentage of the individual's total affiliation with all group members. Using scan sample data of grooming (performed and received), sitting in contact or in close proximity (within 0.5 m), and play, we defined an animal's 'intense' relationships as those within the top quartile of its affiliation scores. 'Weak' relationships

were those within the bottom quartile (cf. Cords & Aureli 1993). For monkeys involved in conflict with partners of both kinds, conciliatory tendency was higher between opponents with intense relationships than between opponents with weak relationships (permutation test: Old group N=15, 56 sums ≥ observed sum, $p<0.01$; New group N=20, 29,952 sums ≥ observed sum, $p<0.05$; adult females: Old group N=9, 2 sums ≥ observed sum, $p<0.01$; New group N=13, 1064 sums ≥ observed sum, $p=0.13$, Fig 4). To ensure there was no sampling artifact, we checked that conflicts with intense and weak partners were represented equally in both groups: in Old group, 24% of sampled conflicts were between animals with an intense relationship, 28% between opponents with a weak relationship; in New group, 28% of opponent-pair relationships were intense, 30% were weak.

The relative intensity of Old group relationships indicated by the analysis of distribution of affiliation is supported by a between-group difference in conciliatory tendency for opponents with intense relationships (Mann-Whitney *U*-test: $N_1=17$, $N_2=27$, $z=2.61$, $p<0.01$; adult females: $N_1=15$, $N_2=22$, $z=1.66$, one-tailed $p<0.05$). In contrast, there was no difference in conciliatory tendency for opponents with weak relationships ($N_1=18$, $N_2=24$, $z=0.20$, NS; adult females: $N_1=12$, $N_2=18$, $z=0.44$, NS).

Furthermore, these analyses confirmed that intense relationships in Old group were not exclusive to related pairs. Even with our broad definition of kinship, only 52.7% of 260 intense relationships in Old group concerned kin (adult females: 57% of 142). Some, 3.4% of 352, weak relationships were between kin (adult females: 4.8% of 176).

Discussion

Reconciliation was demonstrated in two large groups of pigtail macaques confirming results for the same species obtained with a different method by Judge (1991). In both groups former opponents were selectively attracted to each other following conflict, but the groups appeared to differ in other aspects of reconciliation: (1) only in the more recently established group (New) were recipients of aggression more likely to initiate reconciliation, and

Figure 4

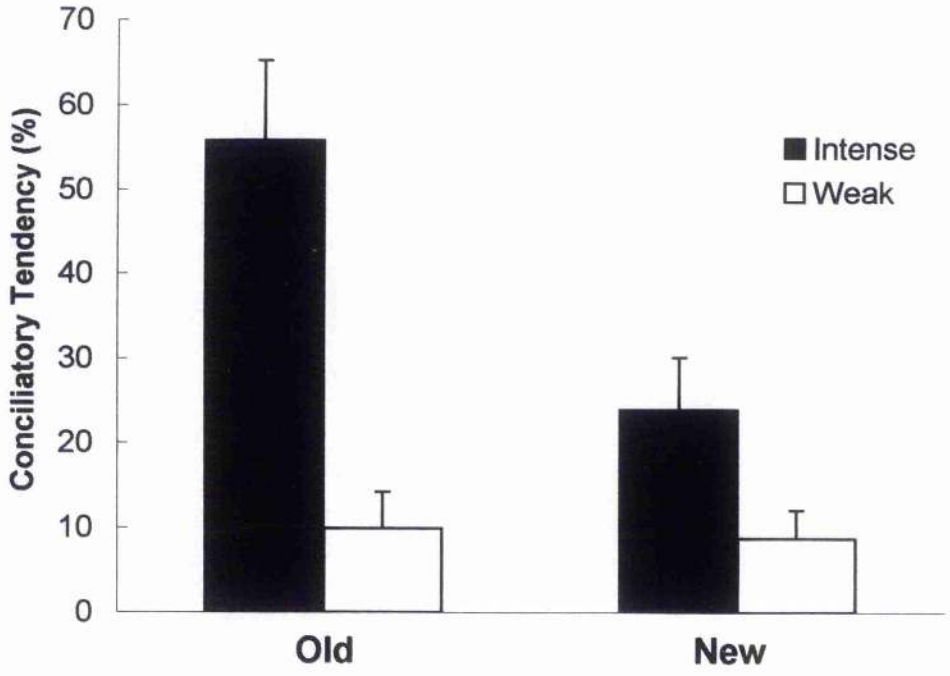

Figure 4. Conciliatory tendency for intense and weak relationships in Old and New groups (x ± SE).

(2) only members of the long-established group (Old) showed specific affiliative acts during post-conflict reunions. In addition, during the 7-month study period, members of Old group showed reconciliation frequencies roughly double those of New group. By contrast, there was no significant between-group difference in individual frequency of other social variables such as allogrooming, approaches, and aggression. However, individuals of Old group affiliated with significantly fewer partners, distributed this affiliation less evenly and, thus, seemed to have more concentrated, less egalitarian social networks than New group animals.

Characteristics of social relationships, such as kinship and level of affiliation, affected conciliatory tendency. In Old group, kin reconciled their conflicts more often than non-kin (no such analysis could be done for New group because of the lack of extensive kin relations) and in both groups conflicts were more frequently reconciled between opponents with relationships characterised by high levels of affiliation.

Initiative and Behavioural Specificity

The between-group difference in conciliatory tendency seemed to be accompanied by differences in the initiative and behavioural specificity of the process. In New group, recipients of aggression initiated proportionally more contacts after a conflict than during control periods. If conciliatory tendency reflects the quality of relationships, as argued here, this may mean that a relatively low value of social relationships is reflected in a lack of conciliatory initiative particularly in dominant individuals. We need to be cautious in the interpretation of these findings, however, as the analysis was based on pooled data due to small sample sizes (see Aureli et al. 1993 for further discussion).

During post-conflict reunions chimpanzees typically kiss one another (de Waal & van Roosmalen 1979), stump-tailed macaques engage in hold-bottom rituals (de Waal & Ren 1988), and Tonkean macaques show clasping gestures (Thierry 1984). These patterns are rarely seen outside the reconciliation context. By contrast, no specific conciliatory behaviour has

been found in other macaque species. Behavioural specificity of post-conflict reunions seems a characteristic of species with a high conciliatory tendency: stumptail and Tonkean macaques show the highest reconciliation frequency of all macaque species studied thus far (Thierry 1986; de Waal & Ren 1988).

Where pigtail macaques fit in this regard is somewhat hard to tell as the results for our two groups differed. In line with the above findings, the group with the higher conciliatory tendency, Old group, showed behavioural specificity, whereas the other group did not. The most typical contact pattern during post-conflict reunions in Old group was 'standing grasp', a behaviour that shares features with the hold-bottom ritual of the stump-tailed macaque.

While 'standing grasp' constituted 19% of the PC contacts in Old group, it never occurred in this group's control observations. In New group, 'standing grasp' occurred almost equally during both PC and MC observations. Between-group differences in behavioural specificity were, therefore, due to the widespread use of 'standing grasp' and other mounting postures in New group and its more restricted use in Old group. Because these contact patterns are likely to reassure the partner, their use in New group outside the reconciliation context may mean that reassuring contact was required more frequently in this group to forestall escalation of tense situations.

Relationship Quality and Social Networks

The relationship quality hypothesis was supported by the post-conflict behaviour of both groups of pigtail macaques. Similar effects were found in captive groups of rhesus (de Waal & Yoshihara 1983) and long-tailed macaques (Aureli et al. 1989; Cords & Aureli 1993), but were not evident in stump-tailed macaques (de Waal & Ren 1988). Our findings strengthen the view that relationship quality affects reconciliation frequency, at least in some species; the relation between the two variables persisted despite a measure of conciliatory tendency that fully controls for baseline levels of affiliation (Veenema et al. 1994).

An important aspect of our study is that between-group variation in relationship quality seems to be directly related to a difference in conciliatory tendency at the group level. Individuals in Old and New groups spent similar amount of time affiliating but the members of Old group directed their affiliation towards fewer partners. Additionally, Old group pigtails distributed their affiliation less evenly. These three findings together lead us to conclude that Old group members had fewer bonds but some of those bonds were firmer. As the most intense relationships in both groups were characterised by a strong conciliatory tendency, the between-group difference in conciliatory tendency seems to reflect the difference in reconciliation frequency with favoured group members. In fact, frequencies of reconciliation were similar for weak relationships in both groups, but were considerably higher in Old group for intense relationships (Fig. 4). Hence, the more concentrated social networks of Old group apparently produced more intense relationships, thus increasing the likelihood of reconciliation.

Group History and Social Networks

The two groups differed in some demographic parameters, such as group size and the number of adult males. These differences could not, however, account for the between-group variation in conciliatory tendency and relationship quality. In fact, analyses limited to relatively homogeneous sub-sets of individuals (i.e. adult females) and corrected for the number of available partners confirmed the between-group variation.

That animals in a long established group distribute affiliation less evenly and among fewer individuals than animals in a more recently established group is intriguing, and, perhaps, non-intuitive. A priori, it is not obvious that animals should affiliate with a greater number of group members when those are relatively unfamiliar. The lack of extensive kin relations in New group was certainly a factor in this distribution, but it cannot be considered an exclusive explanation as the concentrated social networks in Old group were composed of both related and unrelated individuals in roughly equal proportions.

This between-group difference raises the question of how relationships between adult individuals, and consequently whole group affiliation, develop over time. Although New group's demography is unnatural, the process underlying these changes is relevant to situations faced by immigrant individuals and members of groups which split or fuse. We might expect the members of New group to begin to resemble Old group's more concentrated pattern of affiliation in the future. If this does occur, it would suggest that intense relationships are developed at the expense of relationships with other group members. A possible explanation is that prolonged cohabitation produces aversion between certain group members that results in the redirection of affiliation from newly aversive partners to already favoured ones. This process could have the effect of 'raising the stakes' as far as valuable partners are concerned: the fewer affiliates an individual has, the more important it becomes for that individual to stay on good terms with them, so affiliation is increased and conciliatory tendency elevated.

The Systematic Variation Hypothesis

The systematic variation hypothesis that we proposed in the Introduction appears unsupported by our results. The two groups clearly differed in their conciliatory tendency but there was no between-group difference in individual frequency of other social variables such as allogrooming, approaches, and aggression. However, bearing in mind our more refined analysis of affiliative distribution, this apparent lack of systematic variation might be due to the nature of the measures employed to test it. Measures of overall levels of affiliation, such as approach or allogrooming rates, are important indices of social organisation, but how affiliation is parcelled out amongst available partners is equally, if not more, important. For example, Old group's high conciliatory tendency places this group alongside stump-tailed macaques and might, therefore, suggest that pigtail macaques share this species' egalitarian and tolerant dominance style (see de Waal & Ren 1988; de Waal & Luttrell 1989). Yet, our results are hardly suggestive of an egalitarian social structure in Old group. For the

average Old group individual, just eight conspecifics accounted for 69% of total affiliation (53% in New group). Such an individual reconciled conflicts at a high frequency only with a restricted number of group members. The implication of these findings is that the remaining group members are rarely, if ever, affiliates and infrequently receive or confer the benefits of reconciliation after conflicts.

Consequently, the present study also raises questions about the egalitarianism attributed to stump-tailed macaques in the light of their high overall rates of affiliation and tolerance in comparison to rhesus macaques (de Waal & Luttrell 1989). Affiliative behaviour in stump-tailed macaques may follow a pattern similar to that of Old group in the present study, that is, a relatively small number of highly intense social relationships. This possibility requires examination with methods similar to those employed here, but is contradicted by the fact that in stump-tailed macaques neither kinship nor relationship quality affect the frequency of reconciliation (de Waal & Ren 1988; Veenema et al. 1994). This may mean that stump-tailed macaques have high-quality relationships throughout the group, and as a result distribute their affiliative and conciliatory behaviour more evenly. In support of this latter possibility, the pigtail macaques in the present study rated below captive stump-tailed macaques on most affiliative measures (compare Table I of this study with Table I of de Waal & Luttrell 1989; see also Bernstein 1980; Maestripieri 1994). In general, the group life of stump-tailed macaques seems more egalitarian and socially cohesive than that of pigtail macaques.

Variation in group cohesion may depend on the need for intra-group co-operation. In species in which within-group competition over resources is stronger than competition between groups, and in which allies contribute to success in within-group competition, we expect selective social networks, and conciliatory tendencies indexed by relationship quality as in pigtail, long-tailed and rhesus macaques. However, in species in which competition between groups is relatively high, or in which communal defence against predators occurs, fellow group members are important in number: the larger the number of individuals prepared to involve themselves in such

confrontations, the better. In such a situation, indiscriminately high levels of affiliation and/or reconciliation with all partners may be an adaptive social strategy to maintain group cohesion and cooperation (van Schaik 1989; de Waal 1989b).

Our study indicates that between-group and between-species differences follow a pattern that is more complex than previously thought. Previous research (de Waal & Luttrell 1989; Thierry 1990a, b) employed overall rates of behaviour to identify despotic or egalitarian societies. However, individual frequencies of behaviour are sufficient to demonstrate co-variation of traits between groups or species only if the differences are quite dramatic, such as between rhesus and stump-tailed macaques. If differences are less pronounced, more precise measures are needed. Detailed analyses of social networks (i.e. the role of variables such as kinship, rank-distance, size of networks, and so on) provide a tool to investigate the systematic variation hypothesis when variation is subtle, as can occur between groups of the same species. Such analyses provide a much more accurate, but potentially more complex, aid to understanding social organisation. In this study, between-group difference in conciliatory tendency could be directly related to between-group difference in relationship quality. Yet, for Old group pigtails the link between relationship quality and reconciliation, is not mirrored in more egalitarian behaviour towards the average group member, contradicting the prediction of systematic variation. Nevertheless, we do not wish to reject the principle on which systematic variation is based, that is, that traits covary because of variation in relationship quality. In this study, however, the between-group variation in reconciliation behaviour reflected variation in relationship quality, not because all animals in one group behaved in a similar fashion (friendly or antagonistically) towards the average group member, but because animals in one group were more cliqueishly friendly than those in the other.

This study provides further support for the relationship quality hypothesis. The key level for understanding conciliatory patterns is at the relationship level. Differences in reconciliation behaviour within and between groups (or species) reflect differences in the quality of relationships between

their members. While this study implies that high conciliatory tendency within a group (or species) should not be regarded as an unequivocal indicator of egalitarian social organisation, it does illustrate the special usefulness of reconciliation measures as a gauge of social integration.

Chapter 3. BABOON STUDY SITE AND METHODS

Study Site

The study site is situated on the eastern edge of the Laikipia Plateau of Kenya, approximately 40 km north of the town of Nanyuki which lies at the foot of Mount Kenya (0.5° N, 38.8° E). The site, at an altitude of 1,600 to 1,700 metres, can be divided into two halves. The first, Chololo ranch, is privately owned and managed as a cattle ranch. The second half of the study area is the Ndorobo Reserve, an area of land ceded by the Kenyan government to Masai pastoralists. The baboons also occasionally ranged on two other private ranches neighbouring Chololo, Mali and Ol Jogi. The entire area, described in detail by Barton (1989) and Marsh (1992), consists of dry woodland and wooded and bushed grassland, traversed by seasonal watercourses. Precipitous granite outcrops, 'kopjes', exploited by the baboons as sleeping sites, are scattered around the area. *Acacias* are the commonest tree species. At ground level, grasses and sedges such as *Cynodon* and *Kyllinga* predominate, although hardier species, particularly *Sansevieria intermedia*, are typical of the drier areas of the Reserve. Average annual rainfall at the study site is 475.5 mm (1985-1992) and, in this region, there are usually two wet seasons, the 'long rains' - approximately from March to July - and the 'short rains' - from November to December (Ojay & Ogendo 1973). There are man-made dams on both the Ranch and the Reserve, and standing water was available in some parts of the baboons' home range for most of the study period. During the dry season, baboons often dug down into the sandy bases of the seasonal watercourses or exploited deeper waterholes dug by local people. The presence of local people at, and their occasional active defence of, these deeper waterholes meant that access to water was restricted at some times (see Barton et al. 1992; Kenyatta 1995).

As Chololo, Mali and Ol Jogi are primarily managed cattle ranches, human population density is low, consisting of the ranch owners, herders and baboon project research workers. The numbers of cattle are also low -

500 head on the 15,000 acres of Chololo, for example - leaving the ranches as virtual private game reserves. Many species of mammal inhabit the area including zebra, *Equus burchelli*, *E. grevyi*, giraffe, *Giraffa camelopardalis*, elephant, *Loxodonta africana*, cheetah, *Acinonyx jubatus*, leopard, *Panthera pardus*, lion, *P. leo*, and several species of antelope and gazelle (see Barton 1989 for a complete list). The relative abundance of these larger mammals tails off on the Reserve. Here, human population density is higher and, as the people of the Reserve are pastoralists for whom livestock is an important symbol of status and wealth, the Reserve has become overgrazed and subject to serious soil erosion. Goats, sheep and cows are grazed on the Reserve, guarded by herdsmen and their dogs. Feral herbivores are less evident, probably due to the increase in competition and generally poorer grazing, although herds of zebra and gazelle are often found on the edges of the Reserve at dawn and dusk, possibly avoiding the predator rich ranch areas overnight. Some vervet monkeys are present along one riverine forest stretch of the Reserve; but although the baboons sometimes sleep near these vervets, the two species rarely interact or forage alongside each other.

During the study period an adult female baboon and her infant son disappeared suddenly, presumed leopard casualties. One sub-adult female was observed being taken by a pack of dogs from Mali Ranch. Baboons also tended to avoid lions, hyena, cheetah, large snakes, herdsmen and their dogs, though adult male baboons would often chase single dogs away and cheetah were visibly cautious around an entire baboon troop, perhaps in response to human observers. While baboons would pay cursory attention to the larger birds of prey, no alarm calls were observed. As predators, baboons frequently took smaller mammals, particularly cape hares. They also preyed upon immature goat, duiker, dik-dik and Grant's gazelle as well as guinea-fowl, other immature birds and young tortoise. All predation appeared to be opportunistic and all but the youngest baboons attempted and often managed to acquire prey. However, unless a younger predator managed to rapidly consume the prey item or was far from larger baboons, the kill rapidly ended up as the meal of a mature male.

Baboons

Chololo Ranch is home to two long-term baboon projects, which monitor three habituated baboon troops. The Uaso Ngiro Baboon Project (UNBP) is directed by Shirley Strum of the University of California at San Diego. She and her team of Kenyan research assistants mostly concentrate their research efforts on two troops translocated from Gilgil in the Rift Valley District of Kenya to Chololo in 1984 (Strum 1987; Eley et al. 1989). These two troops, Malaika and Pumphouse Gang, have been studied continuously for over 20 years. Members of the Soitoitashe Baboon Project, directed by Andrew Whiten, follow the troop from which the project take its name: Soitoitashe (STT) - Maa for 'White Rocks', one of the troop's sleeping sites. These are an indigenous troop, habituated by Robert Barton in 1986 and continuously studied thereafter. The habituation of all three troops is excellent, permitting close observation (inside 1 m) of all but a few baboons.

I studied STT exclusively. Throughout the research period (April 1994 - April 1995) group demography was tracked following the Gilgil / UNBP protocol (Nicolson 1982; Smuts 1985): Females are labelled adult upon giving birth to their first infant, males when they reach full size and develop a shoulder and upper back cape of hair. A female becomes subadult at her first cycle, a male when he shows signs of the adolescent growth spurt (Watts 1986, 1990) and becomes larger than his mother (generally around 4.5 to 5 years old). Infants are classified as juveniles when they reach 2 years of age. STT's demographic breakdown at the beginning and the end of the study period is presented in Table 1 (together with a measure of the variation during the study). For analyses, individuals were allocated to the age class they belonged to at the mid-point of the data collection period, i.e. November 18, 1994.

Sampling Methods

I collected and analysed three types of data: 1) *standard* focal samples of a selected group of mature individuals, 2) *post-conflict* and *matched control*

Table 1. Demographic breakdown of age-sex classes for STT. Columns indicate number of individuals in each class at the beginning and end of the study, plus the greatest and least number of individuals in each class over the entire period of the study. See text for definitions of classes.

	June 1994	April 1995	Most	Least
Adult Female	17	17	17	16
Subadult Female	4	10	12	4
Juvenile Female	13	7	13	6
Infant Female	2	5	2	5
Adult Male	6	7	7	4
Subadult Male	9	10	11	8
Juvenile Male	15	8	15	7
Infant Male	3	8	3	8
TOTAL	69	72	72	64

focal samples, and 3) *ad libitum* records. For all of these sampling methods, the behaviour and/or presence of dependent infants (under 1.5 years of age) was ignored (except for the special category of 'Infant affiliation' in focal samples). Further details of sampling are provided in the chapters and appendices which follow.

Sampling Schedule

For most of any given data month, standard focal samples were collected on alternate days from post-conflict and matched control samples. Towards the end of a month both types of data were collected during a field day to allow completion of the standard focal sampling rota without the waste of too much field time. After all standard focals had been collected, PC/MC sampling continued and was then practised on consecutive days. *Ad libitum* records were collected on all days.

Dominance Hierarchies

I constructed one overall hierarchy and three 'sub-hierarchies' for STT from *ad libitum* records of dyadic displacement, avoids and aggression. Polyadic data was included when a single individual displaced, was avoided by, or won a conflict against multiple others. The 'overall' hierarchy includes all non-dependent animals who spent at least one month in STT during the study period; the 'male' and 'female' hierarchies are limited to sexually mature animals (sub-adult or adult for the majority of the study period); 'rest' represents the overall hierarchy with mature males removed.

Hierarchies were constructed with an assumption of linearity (i.e. if A is dominant to B and B is dominant to C, I expected A to dominate C) and the aim of minimising reversals (i.e. where A > B > C, but C > A). A short-term immigrant subadult female, Ye, was placed at the bottom of the hierarchy. Juvenile males were placed above the highest-ranking adult female baboon that they outranked but below adult females with whom they had an undecided dominance relationship. (This rule produced a number of reversals as juvenile males tended to be placed lower down the hierarchy

than a number of juvenile females they were clearly dominant to, but prevented those males from being given an artificially high rank, i.e. above adult females whom they had yet to outrank).

To test the assumption of linearity, I employed de Vries's (1995) revised version of Appleby's (1983) procedure which compares the number of circular triads (reversals) in a matrix to the expected number of such triads, given random dominance relationships (de Vries's revision accounts for unknown and tied relationships). For all four hierarchies, linearity could be demonstrated (Overall: N=68, h'=0.457, $p<0.001$; Female: N=25, h'=0.733, $p<0.001$; Male: N=19, h'=0.611, $p<0.001$; Rest: N=49, h'=0.561, $p<0.001$; each randomised 1000 times). The coefficient of linearity (Kendall 1962) varies between the four hierarchies: Female: K=0.71, Male: K=0.58, Rest: K=0.54, Overall: K=0.44. This order reflects the relative number of undetermined dyads in the hierarchies (16%, 23%, 27% and 31% respectively) as Kendall's statistic was designed for complete matrices and, when applied to incomplete data, tends to produce a value of K inversely related to the proportion of undetermined dyads.

These hierarchies represent data from the entire study period. During this period there were a number of large subadult males, both natal and immigrant, in STT; individuals in this class tend to challenge older males and rapidly move up the hierarchy (Strum 1982, 1994; Hamilton & Bulger 1990; Noë & Sluijter 1995). Thus, the lower linearity of the male dominance matrix is, to some extent, a product of relative instability in male-male relations. However, the higher proportion of undetermined male-male dyads and the inherent flexibility of male dominance (e.g. Cheney & Seyfarth 1983) lead me towards a cautious use of these data as independent variables in later analyses such that:

a) a mature male is 'Dominant' to another mature male only if either all *ad lib.* dominance interactions went in his favour or he 'won' at least two more dominance interactions than the other male. (For all other age-sex classes having one more win than another individual was sufficient). If wins were

equal, or a mature male had only one more win, the dyad is regarded as being 'Undecided'. Also, for all age-sex classes:

b) the dominance relationship is 'Unknown' if there were no *ad libitum* interactions between individuals who neighbour each other in the hierarchy.

c) the dominance relationship has been subject to a 'Turnover' if individual A won one, or a series of, interactions with B but then lost a series of two or more interactions to B. If wins alternated, e.g., A beat B, B beat A, A beat B, the relationships is 'Undecided'.

d) 'Rank distance' is the number of individuals ranking between each dyad, plus one. Rank reversals were ignored except when the dyad for which rank distance was calculated was itself a 'Reversal'.

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Chapter 4. POST-CONFLICT BEHAVIOUR OF WILD OLIVE BABOONS. I. RECONCILIATION, REDIRECTION AND CONSOLATION

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Abstract

Observations of post-conflict interactions have provided important insights into primate social organisation. In this study, the nature and determinants of post-conflict behaviour in a troop of wild olive baboons, *Papio anubis*, were investigated. Reconciliation was observed among all age-sex classes, occurring at a rate consistent with a relatively intolerant dominance style. Reconciliation was more frequent when one of the combatants carried a dependent infant but rarely followed conflicts associated with food. Neither the directionality nor the decidedness of conflicts affected conciliatory tendency. In contrast, opponents who were close kin or of similar rank reconciled more often. Olive baboons did not affiliate with non-combatants more frequently following aggression than in control periods, although affiliation with supporters and the close kin of opponents increased. Absence of consolation follows the observed cercopithecine pattern, consistent with the hypothesis that consolation requires an ability to empathise with victim distress. Initiation of post-conflict attacks on third parties was not elevated in victims of aggression. The rarity of redirection is attributed to spatial dispersion, the frequent bidirectionality of baboon aggression and regular

male intervention in female conflicts, all of which appear to limit the availability of 'safe' targets.

Introduction

Among social animals, intra-group resource competition is largely inescapable and, as a consequence, social conflict is unavoidable (van Schaik 1989). While aggression is neither the only form, nor an inevitable expression, of social conflict (Mason 1993), it is the most explicit index of resource competition (Walters & Seyfarth 1987). Aggression is dispersive, stressful and dangerous. However, in non-human primates at least, certain behaviours which occur in the period after aggressive conflict may have evolved to dissipate the negative consequences of aggression. These include: 1) *reconciliation*: peaceful interaction between former opponents; 2) *redirection*: the attack of a previously uninvolved individual by the target of the original aggressive incident, and 3) affiliative interactions between a former opponent and individuals uninvolved in the original conflict, including *consolation* and *substitute reconciliation*.

Reconciliation was the term used by de Waal & van Roosmalen (1979) to label selective affiliative interaction which occurred between former opponents soon after aggression. An increased frequency of such interactions relative to control periods is a feature of the post-conflict behaviour of all but one (ringtailed lemurs, *Lemur catta*: Kappeler 1993) of the wide variety of primate species in which quantitative demonstration has been attempted (reviewed by de Waal 1989b, 1993; Kappeler & van Schaik 1992). Reconciliation can reduce the frequency of received aggression (Aureli & van Schaik 1991b; Cords 1992; de Waal 1993; Castles & Whiten in press b), reduce the rate of behavioural indicators of anxiety (Aureli et al. 1989; Aureli & van Schaik 1991b; Aureli in press; Castles & Whiten in press b) and heart rate (Smucny et al. 1996), and restore tolerance between individuals (Cords 1992).

The frequency of reconciliation varies both within and between species (e.g. de Waal & Luttrell 1989; Castles et al. 1996). Relationship quality (i.e. the strength of inter-individual bonds) is often the best predictor of conciliatory tendency (e.g. Cords & Aureli 1993; Castles et al. 1996). Kinship is one important aspect of relationship quality which has been associated with higher reconciliation rates in several species (e.g. Aureli et al. 1989, 1997; Judge 1991; Call et al. 1996), and such effects can be explained in terms of kin selection theory (Hamilton 1964). However, other variables have been invoked as predictors of reconciliation frequency, including the decidedness of the original conflict, the directionality of the original conflict and the distance between combatants in the dominance hierarchy (Thierry 1986, 1990a; Aureli et al. 1989; Judge 1991; Petit & Thierry 1994a, b).

Redirection of received aggression to a previously uninvolved individual is a common phenomenon among the genus *Macaca* (e.g. Aureli et al. 1993, 1994). Redirected aggression is also used by vervet monkeys (*Cercopithecus aethiops*: Cheney & Seyfarth 1989), subordinate male and immature mountain gorillas (*Gorilla gorilla beringei*: Watts 1995b) and has been attributed to all classes of olive baboons (Smuts 1985), though Eaton (1984) observed no instances of redirected aggression by free-ranging adult and subadult male baboons. Attacking other members of the group soon after receiving aggression can reduce the physiological costs of aggression, divert attention to other individuals (Aureli & van Schaik 1991b) and, if specifically targeted towards the aggressor's kin, allies or favoured mates may levy fitness costs upon the opponent (Aureli et al. 1992).

Increased post-conflict affiliation, or *consolation*, between non-combatants and former opponents has been demonstrated in chimpanzees (*Pan troglodytes*: de Waal & van Roosmalen 1979; de Waal & Aureli 1996). The failure to produce a quantitative demonstration of consolation in other primates has led to the suggestion that consolation is predicated upon the ability to empathise with the distress of combatants, an aspect of a 'theory of

mind' which may be available to apes but no other primates (the Social Cognition hypothesis: de Waal & Aureli 1996). Alternatively, the absence of consolation in macaques may simply reflect differing social constraints upon non-combatants: in comparison with chimpanzees, macaque consolation may be too costly to be adaptive because of an increased risk of receiving aggression when attempting to console and/or reduced benefits from consoling (the Social Constraints hypothesis: de Waal & Aureli 1996).

Other, more specific, forms of post-conflict affiliation have been reported: *substitute reconciliation* (Aureli & van Schaik 1991a), where aggressors increase their affiliation rate with the kin of former opponents, has been demonstrated in captive pigtail macaques, *M. nemestrina* (Judge 1991). Captive patas monkeys, *Erythrocebus patas*, and free-ranging vervet monkeys also affiliate more frequently with the matrilineal kin of opponents following conflict (York & Rowell 1988; Cheney & Seyfarth 1989). In a similar vein, the rate of affiliative interaction between pigtail macaque aggressors and their own kin increased following conflict (Judge 1991) while de Waal & Yoshihara (1983) reported that rhesus macaques, *M. mulatta*, who had bitten their former opponent then elevated their rates of grooming of third parties ('redirected affection'). Such interactions may reflect efforts to reduce the tension associated with conflicts and/or alternative means of restoring relationships via the affiliative networks of former opponents.

Most studies of post-conflict behaviour have concentrated on captive primates. This study details the post-conflict social behaviour of a troop of wild olive baboons. It adds to studies of the closely related chacma baboons (*P. ursinus*: Cheney et al. 1995; Silk et al. 1996) and of wild longtailed macaques, *M. fascicularis*, (Aureli 1992), mountain gorillas (Watts 1995a, b) and moor macaques, *M. maurus*, (Matsumura 1996) by examining the behaviour of both victims and aggressors, and testing the utilisation of post-conflict options beyond reconciliation in a free-ranging cercopithecine population. In addition, the paper explores the effects of rank distance, kinship, and the context and nature of aggression on post-conflict behaviour.

Methods

Study Site

The study site is situated on the eastern edge of the Laikipia Plateau of Kenya, approximately 40 km north of the town of Nanyuki which lies at the foot of Mount Kenya (0.5° N, 38.8° E). The site, described in detail by Barton (1989), is at an altitude of 1,600 to 1,700 metres, and consists of dry woodland and wooded and bushed grassland, traversed by seasonal watercourses. Precipitous granite outcrops, 'kopjes', exploited by the baboons as sleeping sites, are scattered around the area. *Acacias* are the commonest tree species. At ground level, grasses and sedges such as *Cynodon* and *Kyllinga* predominate, although hardier species, particularly *Sansevieria intermedia*, are typical of the drier areas. There are man-made dams throughout the site and standing water was available in some parts of the baboons' home range for most of the study period. During the dry season, baboons often dug down into the sandy bases of the seasonal watercourses or exploited deeper waterholes dug by local people. The presence of local people at, and their occasional active defence of, these deeper waterholes meant that access to water was restricted at some times (Barton et al. 1992; Kenyatta 1995).

Subjects

The subjects of this study were members of an indigenous troop of olive baboons, habituated in 1986 and continuously studied thereafter. The baboons are individually recognisable and habituation is excellent, permitting close observation (inside 1m) of all but a few individuals. Throughout the research period (April 1994 - April 1995) group demography was tracked following the Gilgil / UNBP protocol (Nicolson 1982; Smuts 1985): group size varied from 64 to 72 individuals during the study period due to births, deaths and migration of males and females. There were 16 - 17 adult females, 4 - 7 adult males, 4 - 12 subadult females, 8 - 11 subadult

males, 6 - 13 juvenile females, 7 - 15 juvenile males, 2 - 5 infant females and 3 - 8 infant males. Eleven baboons were born during the study. For analysis, individuals were allocated to the age class they belonged to at the mid-point of the data collection period and individuals were regarded as kin if they were known to be maternal siblings or mother-offspring pairs; all others were considered non-kin.

Data Collection

Data on post-conflict behaviour were collected from 27 June 1994 until 7 April 1995. The method was based on that employed by Aureli et al. (1989), a variant of the original protocol of de Waal and Yoshihara (1983). Post-conflict focal observations (PCs) of between 5 and 15 min duration started immediately after aggressive interactions of any intensity (threat, lunge, chase, chase with contact, bite and fierce bite). Whenever such aggressive interactions were witnessed, the nature of the aggressive incident was recorded: the *victim* was the individual initially attacked, its *main aggressor*, the opponent which attacked most intensively and longest. Also noted were the identities of supporters and other opponents, together with the highest intensity of aggression displayed by each opponent, the response to aggression, the outcome of the conflict (aggressor wins, loses, or draws) and the context of the aggressive incident. A conflict was won if one opponent unilaterally withdrew or submitted; it was drawn if the recipient of aggression countered with aggression and no clear signs of submission were shown by either opponent. For each PC one of the combatants was selected as a focal subject. Twenty-three individuals (8 adult, 2 subadult females and 7 adult, 6 subadult males) selected for standard focal observations (not analysed here) had priority over all others. Beyond this criterion adults and subadults were preferred to younger subjects, a balance between initiators and recipients of aggressive incidents was attempted, and individuals rarely involved in aggression were favoured subjects. PCs were

restarted if aggression recurred within 30 seconds of starting the PC focal observation.

During the PC, all agonistic and affiliative interactions in which the focal individual was involved were recorded continuously. Affiliative interactions comprised approaches resulting in nonaggressive contact or exchange of affiliative signals - grunting, lipsmacking, and 'come-hither' face (Strum 1987). Interactions with individuals younger than 1.5 years of age were ignored.

Instantaneous point samples were taken after the first minute of the PC had elapsed and every 60 s thereafter. We recorded the activity of the focal animal as follows (based on van Schaik et al. 1983):

1. Drink / Eat / Forage - any of drinking; processing or eating food from a clumped food source (mainly fruit); and handling or eating from a dispersed food resource (mainly grass or herbs). These three categories were combined for analyses because 'drink' and 'eat' were rarely scored (less than 2% of all point samples).

2. Travel - moving rapidly in a consistent direction.

3. Travel Search - moving while scanning the environment, apparently for food.

4. Immobile - sitting, lying, resting, standing while eyes open or closed.

5. Social - copulating, being involved in affiliative or aggressive interactions.

6. Other activities.

Finally, the distance of the focal individual to the opponent(s) at both the beginning and end of the PC and changes in proximity during the PC

were noted. Proximity was split into 5 grades - within 0.5 m, between 0.5 m and 2 m, between 2 m and 5 m, between 5 m and 10 m, and over 10 m apart.

A matched control observation (MC) of the same duration as the PC was made of the same subject on the next observation day (there were never more than 5 days between a PC-MC pair). Control observations, methodologically identical to PCs, were begun within 30 min (either side) of the start time of the PC. The opponent(s) of the focal subject had to be within view or within 100 m of the focal at the beginning of the MC; i.e. within the focal individual's group or sub-group. If any of these conditions were not met the MC was postponed until the next observation day. Additionally, MCs were postponed if the focal animal was involved in aggression in the 3 minutes prior to a planned observation.

PC-MC observations were recorded on tape cassette, timed by electronic stopwatch and later transcribed to computer files. All data were collected by the first author.

Analysis

A total of 454 PC and MC observations were collected on 56 different focal subjects. The mean duration of PCs was 14.6 min; there were 450 of at least 10 min duration. In some PCs the focal subject had more than one opponent, so that this method produced data on 590 PC-MC opponent-pairs (mean = 10.5 per focal subject; range = 1 - 33); 85% of these comprised unique aggressor-victim dyads.

To demonstrate the existence of social events characteristic of post-conflict situations we used both the method described by de Waal & Yoshihara (1983), which we will refer to as the 'PC-MC method' and that developed by Aureli et al. (1989) and Aureli & van Schaik (1991a), which we will refer to as the 'time rule'. Under the 'PC-MC method', we assessed whether a pair of former opponents engaged in affiliative interaction during the PC only, or earlier during the PC than during the MC: 'earlier' pairs. If such interaction occurred in the MC only, or earlier in the MC than in the PC

then the pair was labelled 'later'. Finally, we compared the proportion of each individual's earlier and later pairs using the Wilcoxon signed ranks test (Siegel & Castellan 1988).

When following the 'time-rule', we determined for each PC and MC observation the minute in which the first affiliative interaction between former opponents occurred. Next, we compared the distribution of first PC events to first MC events using the Kolmogorov-Smirnov test (Siegel & Castellan 1988). If this test produced a significant result we then ran a Wilcoxon signed ranks test comparing individual PC and MC scores within the time period in which the PC distribution differed from that for the MC. In this way we ensured that differences in the distribution of first PC and MC events were not due to the extreme behaviour of a few individuals. 'Time-rule' analyses are restricted to the first 600 sec of PC-MC pairs of at least that duration.

When comparing reconciliation frequency across classes of individuals, we employed Veenema et al.'s (1994) revised measure of Conciliatory Tendency (a measure of reconciliation frequency that fully controls for baseline levels of affiliation). Conciliatory Tendency for a focal individual = $(e - l) / t$, where e is the number of earlier pairs, l is the number of later pairs, and t is the total number of PC-MC pairs for that individual. Conciliatory Tendency is measured per focal individual regardless of whether it was this individual or its opponent that initiated the interaction.

Ideally, multivariate statistics would allow the contribution of each factor potentially affecting post-conflict interaction to be assessed simultaneously. However, this data set does not meet the assumptions of such tests, so hypotheses were investigated independently using non-parametric tests. Whenever possible, analyses were conducted at the individual level on subjects with at least 3 qualifying PC-MC pairs. Where small sample sizes made this impossible, we either relaxed the 3 PC-MC pair rule or used Chi-square or G tests (Sokal & Rohlf 1981) on pooled data, checking that significant results were representative of the behaviour of most

individuals. Analyses were two-tailed except when otherwise stated and the significance level was 5%.

Results

Reconciliation

The demonstration of reconciliation

Following the PC-MC method, the proportion of earlier pairs was greater than that of later pairs when analysed at the individual level (16.7% vs. 1.2%; Wilcoxon signed ranks test: N=49, z=5.23, p<0.001). Mean conciliatory tendency was 15.6% (N=50, SD=15.3%).

According to the time-rule, former opponents affiliated significantly sooner after the end of the conflict than in control periods (Fig. 1; Kolmogorov-Smirnov test: D=0.40, one-tailed p<0.05); the greatest difference in the cumulative distributions occurred after four minutes. This was confirmed at the individual level as most focal individuals were involved in affiliation with former opponents more often in the first four minutes of PCs than in the first four minutes of MCs (Wilcoxon signed ranks test: N=49, z=4.94, p<0.001). Time-rule data are based on dyadic conflicts; for polyadic conflicts PC curves closely resembled those for dyadic conflicts. Taken together, these results demonstrate that former opponents contacted each other sooner in the PCs than MCs.

Selective attraction

It is possible that the increase in PC affiliation was non-selective, i.e. that animals involved in a conflict increased their affiliation rates with all members of the group, not just their former opponents. To test this possibility, we examined all of the focal animal's affiliative interactions in the PC and MC, ignoring initiative. Focal animals observed in at least 3 PCs were involved in 1,279 PC and 1,163 MC affiliative interactions; a non-significant increase of 10.0% (Wilcoxon signed ranks test: N=45, z=1.60, p>0.1). Former opponents were the focal's partner in 16.0% of PC affiliative

Figure 1

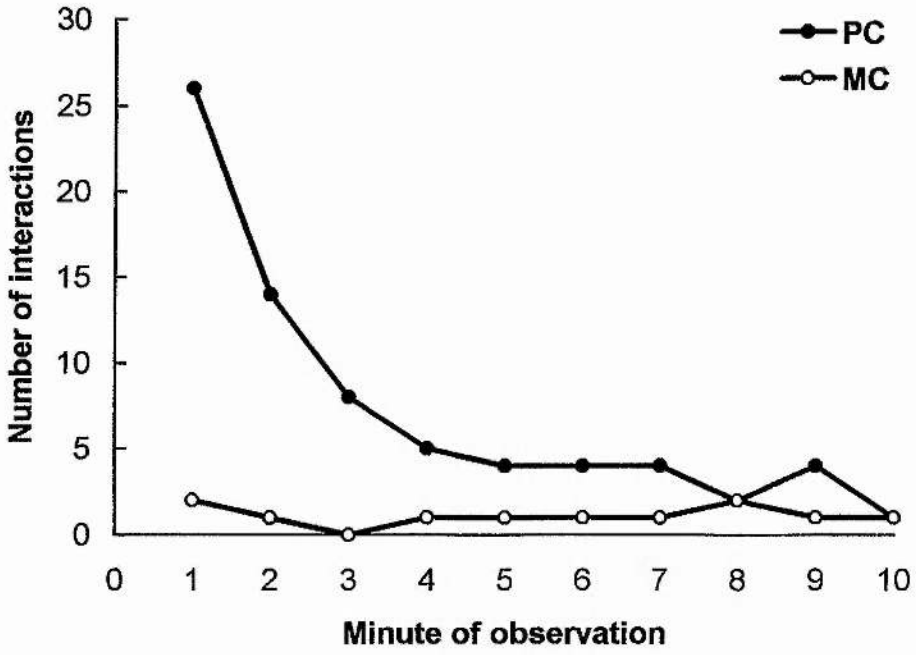

Figure 1. Distribution of the first affiliative interaction between former opponents during the first 10 min of the post-conflict (PC) and matched control (MC) observations.

interactions but just 2.2% of MC acts (Wilcoxon signed ranks test: N=45, z=4.98, p<0.001), demonstrating that the increase in post-conflict affiliation was highly selective.

Distance

It is possible that former opponents were more likely to affiliate after a conflict simply because they were closer to each other than they may have been in MC observations. To control for this, we examined the proportion of earlier and later pairs for each focal individual in only those PC-MC pairs in which the distance to their opponent was the same at the beginning of the PC as of the MC. There were 195 such opponent pairs and within these there was a higher proportion of earlier than later pairs (12.5% vs. 0.3%; Wilcoxon signed ranks test: N=29, z=3.18, p<0.005), establishing that the constraints of MC distance on opportunity to affiliate were not responsible for increased post-conflict affiliation.

Initiative

We investigated whether recipients of aggression were more likely to initiate conciliatory interactions than other affiliative interactions. The analysis was limited to conflicts in which the direction of aggressive behaviour was unambiguous (i.e. excluding incidents with mutual aggression). First, we calculated the proportion of approaches made by recipients of aggression leading to the first affiliative interaction between former opponents in PCs. We compared this figure to the proportion of all approaches leading to affiliative interaction between former opponents in the corresponding MCs. Due to small sample sizes in the MCs, we could not examine the difference between the two proportions at the individual level. Testing pooled data revealed no significant difference: 38% of 99 first PC interactions were initiated by the recipient of aggression vs. 50% of 36 interactions in the MCs (G=1.27, df=1, p>0.2).

Specific affiliative acts

Figure 2 compares the distribution of specific conciliatory acts (first contact or first exchange of affiliative signal; N=99) during the first PC affiliative interaction between former opponents with the distribution of specific acts in all affiliative interactions for the same dyads in the corresponding MCs (N=36). There was no significant difference between these distributions (χ^2=13.13, df=7, p>0.05).

Sex & Age

Conciliatory tendency (CT) was not significantly affected by the age class of former opponents. CTs of individuals with a particular age class opponent were calculated when there were at least 3 PCs for that individual with opponents in that age class. These CTs were classified according to the age of the individual and opponent, and the CTs for each of these categories compared using a Kruskal-Wallis One Way ANOVA (Fig. 3; χ^2=4.92, df=5, p>0.4). Similarly, the sex of opponents did not significantly affect conciliatory tendency (Fig. 4; K-W: χ^2=4.74, df=2, p>0.09).

Kinship

Few conflicts between known kin were sampled, so analysis at the individual level is impossible. However, according to a pooled analysis opponents that were kin reconciled at significantly higher frequencies (9 earlier, 0 later from a total of 18 PC-MC pairs) than unrelated individuals (85 earlier, 11 later from a total of 487 PC-MC pairs; Gadj.=11.07, df=1, p<0.001).

Rank Distance

A linear dominance hierarchy was constructed from opportunistic records of dyadic displacement, avoidance and aggression. Polyadic data were included when a single individual displaced, was avoided by, or won a conflict against multiple others. We confirmed that the hierarchy was linear

Figure 2

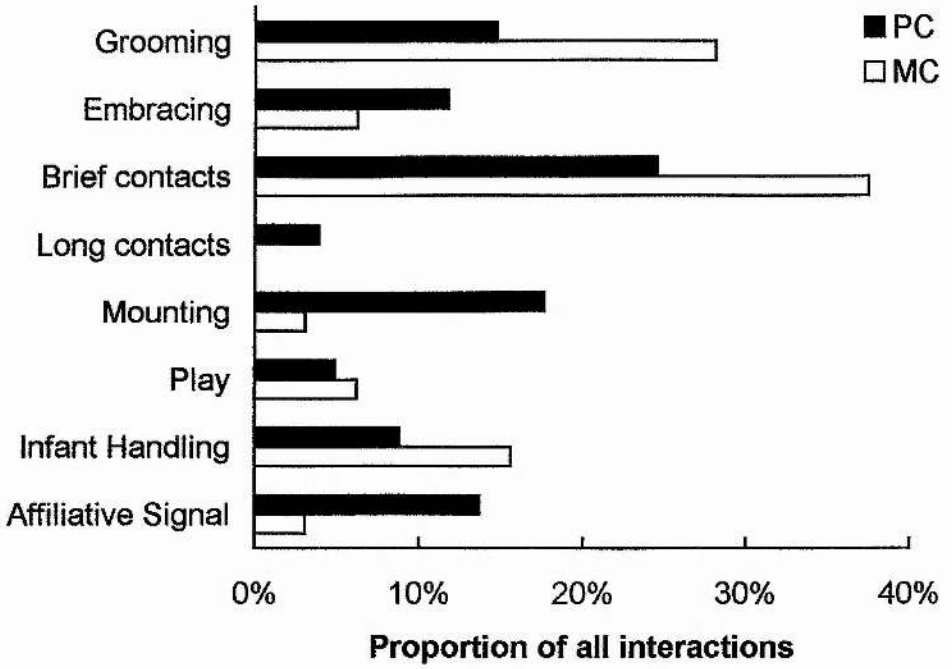

Figure 2. The occurrence of eight classes of affiliative act among the first affiliative acts between former opponents during post-conflict observations (PC) and among all affiliative acts between the same two individuals during matched control observations (MC). The frequencies are expressed as a percentage of the number of such acts scored during PCs (n = 99) and MCs (n = 36).

Figure 3

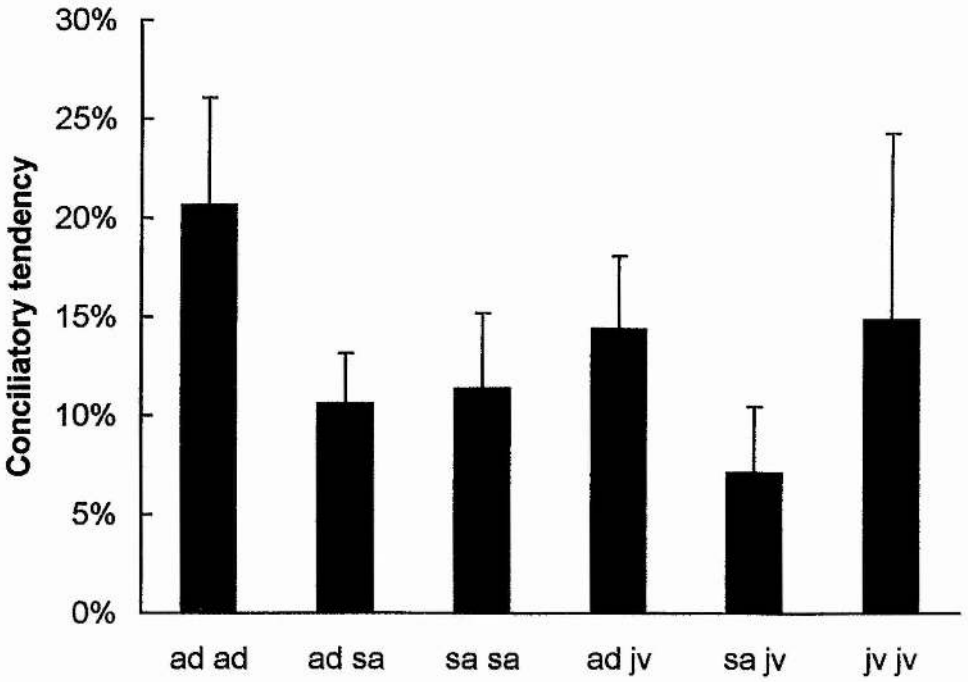

Figure 3. Conciliatory tendencies following conflicts between opponents of six age class permutations (ad = adult, sa = subadult, jv = juvenile; x ± SE).

Figure 4

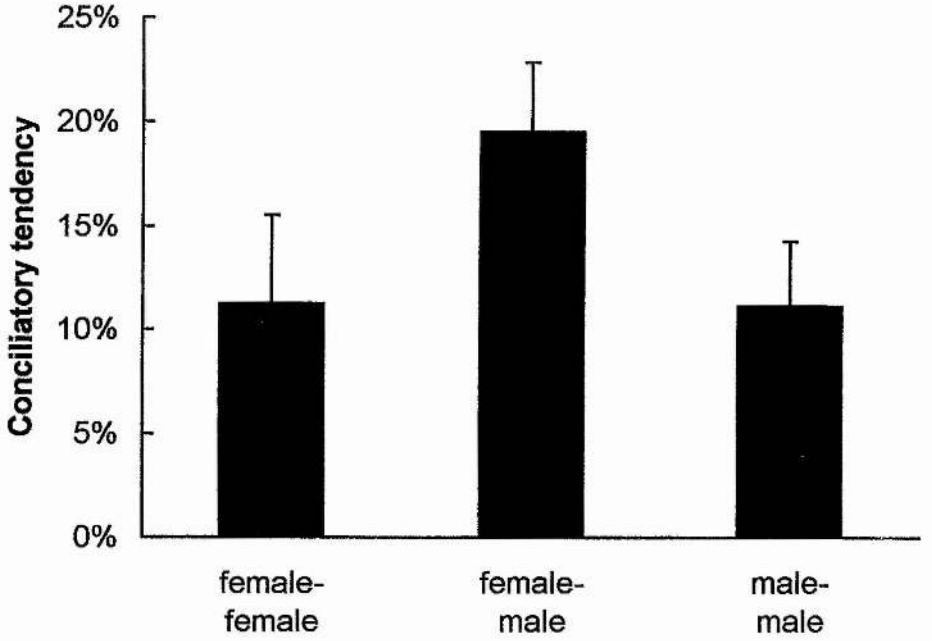

Figure 4. Conciliatory tendencies following conflicts between females, males and between the sexes (x ± SE).

(N=68, h'=0.457, $p<0.001$) by employing de Vries's (1995) revised version of Appleby's (1983) procedure which compares the number of circular triads (reversals) in a matrix to the expected number of such triads, given random dominance relationships. 'Rank distance' is the number of individuals ranking between a dyad, plus one.

We assessed the effect of rank distance on conciliatory tendency by allocating each opponent pair to one of 12 rank distance categories (1-5, 5-10, 10-15,....., 50-55, 56-64) and calculating the CT for all opponent pairs within each rank distance class. CT declined as rank distance increased (Fig. 5; Spearman's Rank: $r_s=-0.76$, N=12, $p<0.01$). At the individual level, conflicts between baboons less than 21 ranks apart had a significantly higher CT than those separated by over 30 ranks (14.9% vs. 5.1%; Wilcoxon signed ranks test: N=17, z=1.85, one-tailed $p<0.05$; for individuals with at least 3 PCs in both rank classes). Note that this division was made such that a roughly equal number of opponent pairs were in each category.

Context

The context in which the original aggressive incident occurred affected the likelihood of reconciliation. Three contexts were common: 'food' - when either opponent had been foraging or eating when the conflict began (114 opponent pairs); 'infant' - when either opponent had a dependent infant (60 pairs); and 'none' - when there was no obvious context to aggression (375 pairs). Six pairs which qualified as both food and infant conflicts were analysed as infant conflicts. Figure 6 illustrates conciliatory tendency at the group level for the three contexts. Analysing these differences at the individual level with no criterion for the minimum number of opponent pairs, we found that aggression associated with food was less frequently reconciled than when there was no context to aggression and that 'infant' conflicts were more frequently reconciled than 'food' conflicts, particularly when they were between females (no context vs. food: 16.9% vs. 1.0%; Wilcoxon signed ranks test: N=39, z=2.99, $p<0.005$; infant vs. food: 20.2%

Figure 5

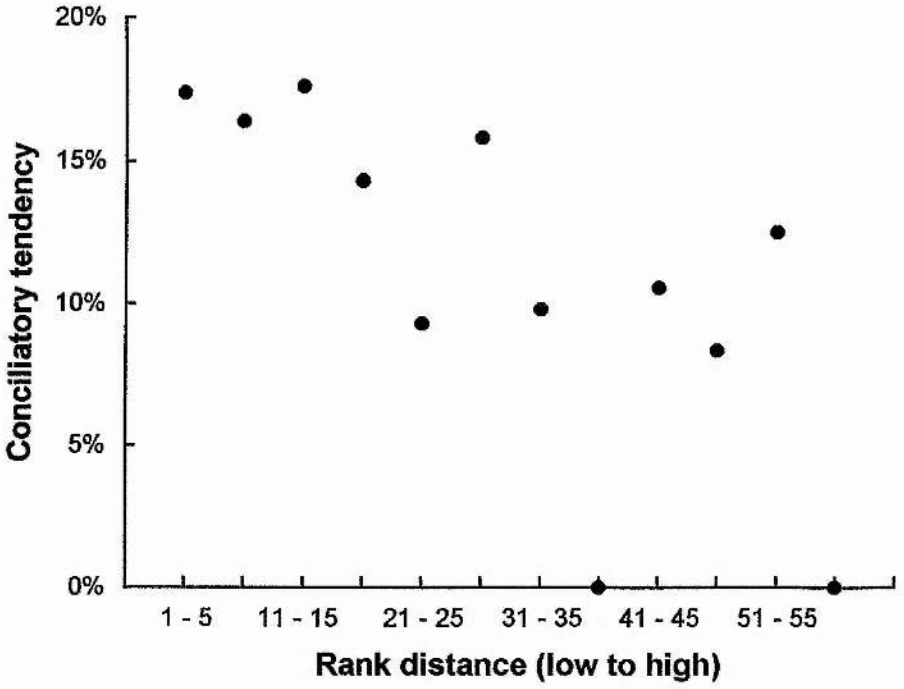

Figure 5. The relationship between conciliatory tendency and rank distance.

Figure 6

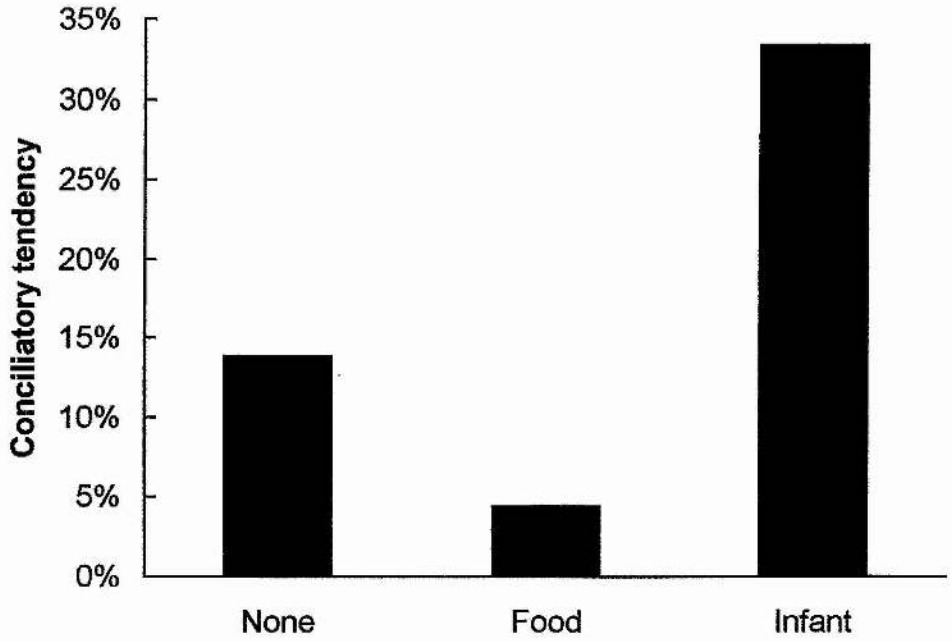

Figure 6. Group level conciliatory tendency following conflicts in which at least one opponent carried a dependent infant, when either opponent had been foraging or eating when the conflict began, and when there was no obvious context to aggression.

vs. 1.0%; N=18, z=2.07, p<0.05; female-female infant vs. food: 41.6% vs. 4.0%; N=10, z=2.07, p<0.05).

Decidedness & Directionality

A conflict was 'decided' if it had a clear winner and it was 'unidirectional' if only one opponent delivered aggression. Neither the decidedness of the conflict nor the directionality of aggression affected reconciliation frequency. The proportion of earlier pairs following drawn conflicts (8/52, 0 later pairs) was very similar to that following decided conflicts (86/538, 11 later pairs; G=0.01, df=1, p>0.9). Similarly, conflicts involving counter-aggression were no more likely to be reconciled (22 earlier, 1 later, 145 total pairs; mean CT=16.9%) than those in which only unidirectional aggression occurred (72/445, 10 later; 14.3%; Wilcoxon signed ranks test: N=18, z=1.41, p>0.15).

Intensity

The intensity of the original conflict did not affect post-conflict conciliatory tendency. Low intensity conflicts (threats and lunges: 158 pairs; mean CT=15.1%) were equally likely to be followed by reconciliation as high intensity conflicts (chases, grappling, biting and bi-directional conflicts: 432 pairs; mean CT=15.2%; Wilcoxon signed ranks test: N=44, z=1.23, p>0.2). Finer categorisation of conflict intensity did not affect this result.

Redirection of Aggression

To quantitatively demonstrate the occurrence of redirection it must be shown that recipients of aggression initiate attacks on third parties in post-conflict periods more frequently than they initiate attacks in control periods. In this study, baboons who received a bout of aggression during the original conflict were not more likely to attack an individual uninvolved in the initial conflict earlier in the PC than in the MC. (mean proportion of earlier pairs = 6.0%, later = 7.4%; Wilcoxon signed ranks test: N=32, z=0.13, p>0.85). Likewise,

there was no difference in the PC and MC distributions of first aggressive interactions with a previously uninvolved baboon (Fig. 7; K-S test: D=0.14, NS). Some redirected aggression occurred before the PC began, i.e. during the initial aggressive incident; adding these cases to the analyses did not significantly alter this result (10.5% earlier, 6.1% later; Wilcoxon signed ranks test: N=32, z=1.60, p>0.1).

Consolation

Using the PC-MC method we found no tendency for focal animals to affiliate more frequently with individuals other than their former opponent(s) following a conflict than in a matched control period (42.4% earlier vs. 35.7% later pairs; Wilcoxon signed ranks test: N=45, z=1.60, p>0.1). Time-rule analysis confirmed this result (Fig. 8; K-S test: D=0.11, NS).

Further analyses require PC-MC pairs to be distinguished according to the role of the focal animal in the initial conflict: 'aggressors' are animals who initiated a dyadic or all polyadic conflicts preceding a PC in which no counter-aggression was received (175 PC-MC pairs). 'victims' are animals who received aggression without retaliating or initiating a further conflict prior to the PC (173 pairs).

Neither victims nor aggressors increased affiliation with non-opponents following a conflict (aggressors: 34.4% earlier vs. 38.9% later pairs; Wilcoxon signed ranks test: N=25, z=0.38, p>0.7; victims: 47.7% vs. 34.8%; N=21, z=1.32, p>0.15). Furthermore, there was no significant difference in the distribution over time of first affiliative interactions in the PC and MC (K-S tests: aggressors: D=0.05, NS; victims: D=0.19, NS). Relaxing the definitions of victim and aggressor to include bidirectional conflicts did not alter these results.

There was no tendency for either unilateral victims or aggressors to initiate the first affiliative interactions with a non-opponent more often in the PC than in the MC. Aggressors initiated 50% of 100 PC interactions and 57% of 96 interactions in the MCs (G=1.05, df=1, p>0.3); victims initiated

Figure 7

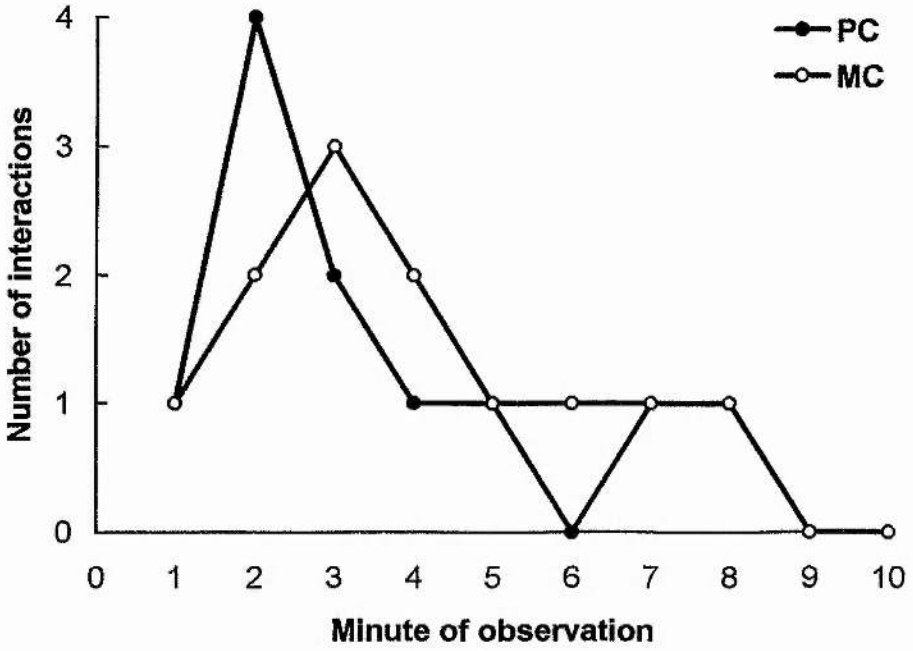

Figure 7. Distribution of the first aggressive act directed by victims against group members other than the former aggressor in the first 10 min post-conflict (PC) and matched control (MC) observations.

Figure 8

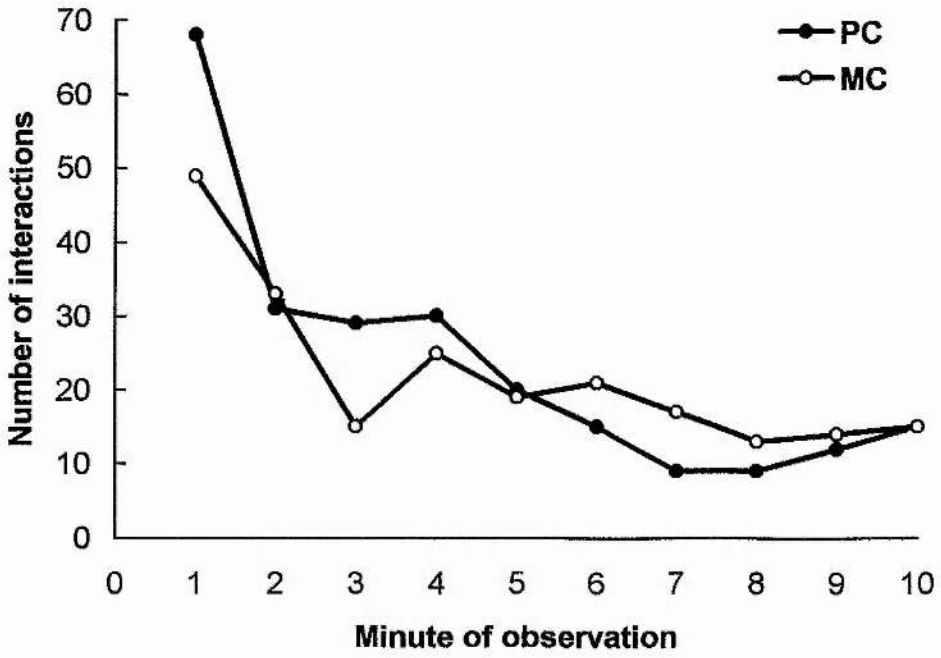

Figure 8. Distribution of the first affiliative interaction between the focal combatant and group members other than the former opponent in the first 10 min post-conflict (PC) and matched control (MC) observations.

50% of 112 first PC interactions and 47% of 99 MC interactions (G=0.13, df=1, p>0.7).

Post-conflict Kin-Oriented Affiliation

Affiliation with own kin

We investigated whether baboons increased affiliation with their own kin following a conflict by examining the 385 PC-MC pairs in which the original conflict had been between non-kin and where the focal animal had kin. There was no difference between the proportions of earlier and later pairs (9.5% vs. 6.5%; Wilcoxon signed ranks test: N=38, z=1.11, p>0.25). In contrast, time-rule analysis (PCs of at least 600s) did indicate a difference in the distribution of affiliative interactions (Fig. 9; D=0.48, p<0.005); the greatest difference in the cumulative distribution was within the first five minutes. However, affiliation with kin was infrequent (just 9.5% of all PC and 4.6% of MC affiliative interactions for observations of individuals with kin) and it appears that the post-conflict behaviour of just one female (contributing 10 of 44 first affiliative interactions with kin) was responsible for this result as we could not confirm this result at the individual level: most focal individuals were not involved in affiliation with kin more often in the first five minutes of PCs than in the first five minutes of MCs (Wilcoxon signed ranks test: N=38, z=1.19, p>0.2).

Neither unilateral aggressors nor unilateral victims affiliated earlier with kin in the PC than in the MC (aggressors: 7.2% vs. 11.3%; Wilcoxon signed ranks test: N=18, z=0.84, p>0.4; victims: 14.1% vs. 6.1%; N=19, z=1.68, p>0.05). Also, there was no difference in PC and MC latency to affiliate for either unilateral aggressors (116 PCs; D=0.4, NS) or unilateral victims (144 PCs; D=0.58, NS).

Affiliation with opponent's kin

In contrast, baboons did increase their affiliation with the kin of their opponents after a conflict. We examined the 380 PCs in which the focal's

Figure 9

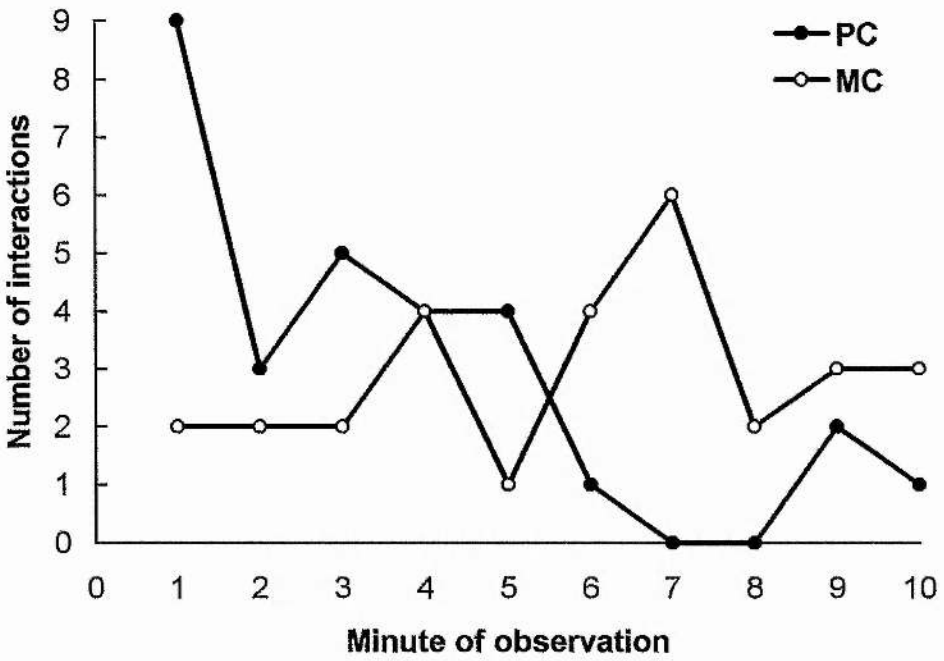

Figure 9. Distribution of the first affiliative interaction between the focal combatant and its own kin in the first 10 min post-conflict (PC) and matched control (MC) observations.

opponent had kin. Individuals affiliated earlier with their opponent's kin in the PC than in the MC (4.7% vs. 1.9%; Wilcoxon signed ranks test: N=42, z=1.96, p=0.05). Time-rule analysis on the 376 qualifying PCs failed to support these results (Fig. 10; K-S test: D=0.67, NS), but there were too few interactions with opponent's kin in the MC sample for reliable testing and the distribution is suggestive of a small effect. Affiliation with the opponent's kin accounted for 2.8% and 1.4% of all PC and MC affiliative interactions respectively.

When the data set was broken down to unilateral aggressors and unilateral victims, increases in affiliation with the opponent's kin could not be demonstrated (aggressors: 3.4% vs. 1.4%; Wilcoxon signed ranks test: N=23, z=0.94, p>0.3; victims: 3.0% vs. 1.2%; N=17, z=0.81, p>0.4), but the effect may nevertheless be shared by both: unilateral victims had 10 earlier and 2 later pairs, aggressors 7 and 2.

There were too few affiliative interactions with the kin of opponents in MCs for statistical analysis, but in PCs there was a marked tendency for opponents' kin to initiate interactions (17 of 22 interactions). This was particularly pronounced for victims of aggression who initiated just 2 of 14 interactions with their opponent's kin. No specific behaviour predominated these interactions.

Affiliation with Supporters

There were 46 PCs in which the focal animal was supported by at least one other individual. In these, supported baboons were involved in affiliative interaction with individuals who had supported them in the original conflict earlier in the PC than in the MC (26.7% vs. 0%; Wilcoxon signed ranks test: N=24, z=2.66, p<0.01). The distribution over time of first interactions between former supporters is illustrated in Fig. 11, but as there were no interactions between former supporters in the MC a K-S test could not be carried out. Most interactions (10 of 14) were between a mature (adult or older subadult) female and a mature male. In these interactions, the male,

Figure 10

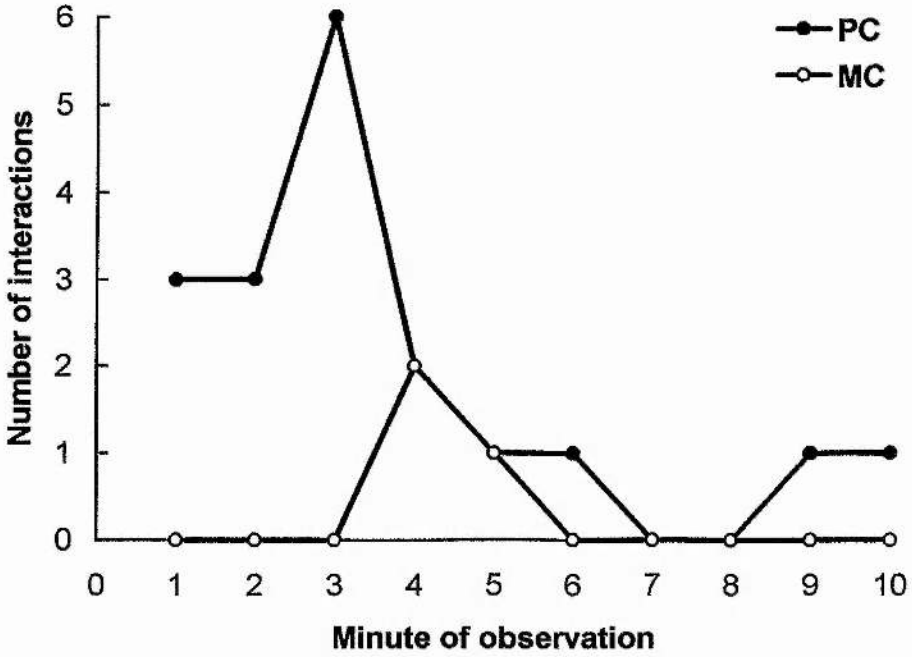

Figure 10. Distribution of the first affiliative interaction between the focal combatant and the kin of its opponent in the first 10 min post-conflict (PC) and matched control (MC) observations.

Figure 11

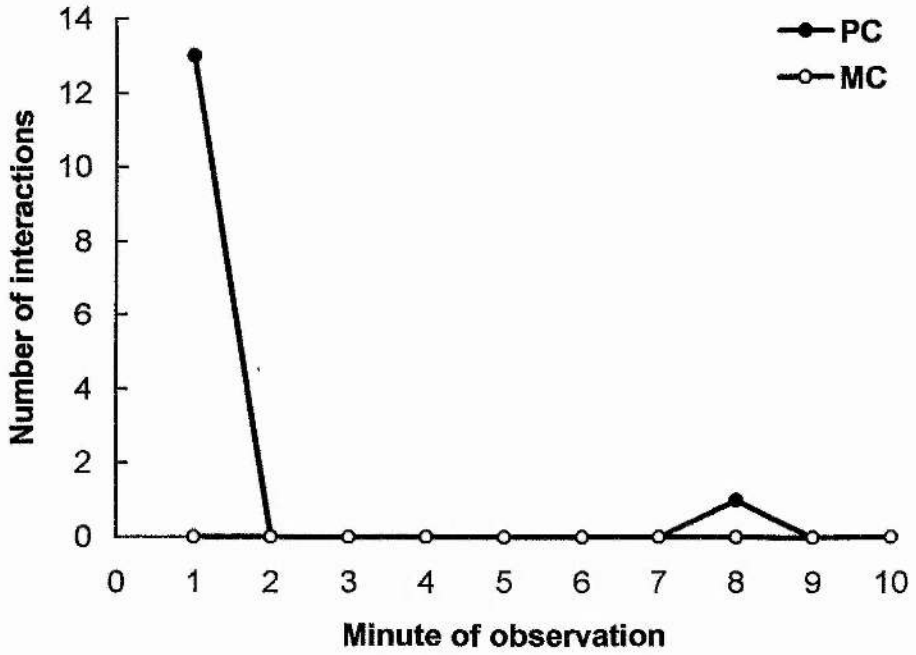

Figure 11. Distribution of the first affiliative interaction between the focal combatant and group members who provided agonistic support during the original conflict in the first 10 min post-conflict (PC) and matched control (MC) observations.

always the supporter in the original conflict, usually (9 times of 10) initiated affiliative contact, which frequently led to the female grooming the male (7 of 10).

Consequences of aggression for activity budgets

We compared the activity budgets of baboons following aggression to that in matched control periods, excluding PC-MC pairs in which reconciliation occurred. When all conflicts were analysed together, only the rate of 'travel/search' behaviour was reduced following conflict (Fig. 12; Wilcoxon signed ranks test: N=53, z=2.19, $p<0.05$). Both unilateral aggressors and unilateral victims exhibited this difference (Fig. 13a & b; aggressors: n =36, z=2.68, $p<0.01$; victims: N=39 z=2.36, $p<0.05$). Aggressors alone had higher rates of 'eat / forage' following a conflict (N=36, z=2.74, $p<0.01$). Comparing the post-conflict activity budgets of individuals who were both unilateral aggressors and unilateral victims, we found that baboons travelled more when they had been victims (N=26, z=2.98, $p<0.005$) and foraged more when they had been aggressors in the original conflict (N=26, z=2.62, $p<0.01$).

Discussion

Reconciliation was demonstrated in a population of free-ranging olive baboons. Mean conciliatory tendency was 15.6%. If one of the combatants had been eating or foraging when aggression began, conciliatory tendency was markedly reduced but otherwise the nature of the conflict did not affect reconciliation frequency. In contrast, aspects of the relationship between combatants did influence reconciliation: closely related animals were more likely to reconcile conflicts than more distantly or unrelated individuals, individuals who ranked closer to each other in the dominance hierarchy also reconciled a higher proportion of conflicts. Aggression affected the activity budget of combatants: aggressors were more likely to forage after conflicts while victims spent more time travelling.

Figure 12

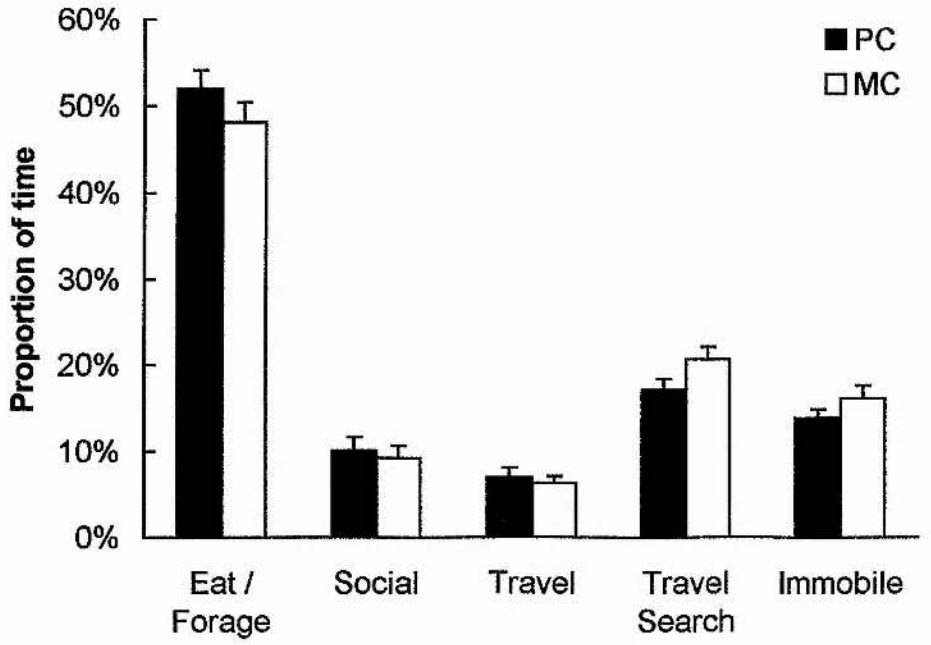

Figure 12. Activity budgets in the first 10 min post-conflict (PC) and matched control (MC) observations (x ± SE).

Figure 13

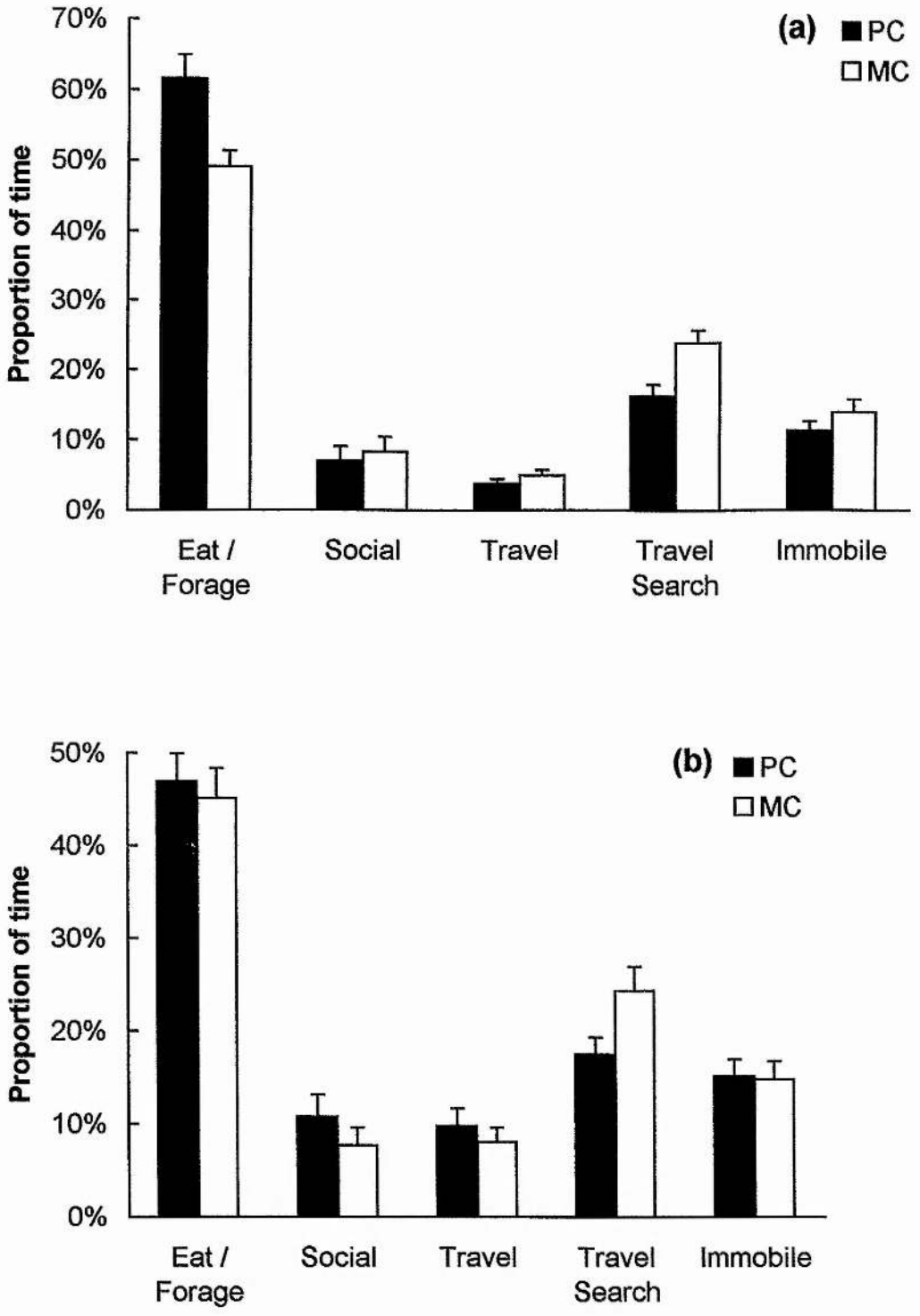

Figure 13. Activity budgets of (a) unilateral aggressors and (b) unilateral victims in the first 10 min post-conflict (PC) and matched control (MC) observations (x ± SE).

Neither victims nor aggressors were any more frequently involved in post-conflict affiliative interactions with non-combatants in general. However, there was evidence that both victims and aggressors were more likely to affiliate with the kin of former opponents following aggression. They were also more likely to affiliate with individuals who had supported them in the original conflict. Redirection of aggression to uninvolved individuals by victims was rare and did not occur any more frequently than in control periods.

Demonstrating Reconciliation

Free-ranging olive baboons were selectively attracted to each other following some conflicts, rapidly engaging in affiliative interaction. The results further confirm the generality of reconciliation in primates, consistent with field studies by Aureli (1992), Watts (1995a), Matsumura (1996), and Silk et al. (1996). The conciliatory behaviour typical of post-conflict situations in most captive primates is clearly paralleled by wild olive baboons. Furthermore, the details of baboon conciliatory behaviour fit with general theoretical trends emerging from captive studies, which we now discuss in more depth.

The nature of reconciliation

On the basis of evidence presented by Thierry (1985; 1986; 1990a), de Waal (1989b; 1993), and from captive pigtail macaques, Castles et al. (1996) argue that conciliatory tendency is a valuable index of a population's 'dominance style', which essentially refers to how tolerant dominant individuals are of lower-ranking conspecifics (de Waal & Luttrell 1989). While dominance style is likely to be influenced by prevailing ecological and demographic conditions, and thus generalisation from one group should be treated with caution, this group's conciliatory tendency, at just 15.6%, suggests that high-ranking olive baboons are relatively intolerant of subordinates. Given this, it is not surprising that in this population the

recipients of aggression initiated fewer conciliatory interactions than the original aggressors as low rates of conciliatory tendency tend to be associated with low rates of victim initiation (de Waal 1993). However, it is important to compare frequency of victim initiation of conciliatory episodes with the rate for affiliative interactions in control periods, and baboons did not differ in this respect. If dominance relationships are usually relatively intolerant then we might expect victims of conflict (usually subordinate individuals) to be constrained in their ability to initiate reconciliation (de Waal & Ren 1988). This may be particularly pertinent to baboons given the increased risk of receiving aggression in the period before reconciliation (Castles & Whiten in press b; cf. Aureli et al. 1989).

In captive studies, distinctive conciliatory behaviour is associated with particularly tolerant, frequently reconciling populations: kissing in chimpanzees (de Waal & van Roosmalen 1979), clasping gestures in Tonkean macaques, *M. tonkeana*, (Thierry 1984), the hold-bottom ritual of stumptail macaques, *M. arctoides*, (de Waal & Ren 1988), and the standing-grasp of a high conciliatory tendency pigtail macaque group (Castles et al. 1996). Baboons did not appear to use any behaviour preferentially in conciliatory interactions. Thus, in concordance with their relatively low conciliatory tendency, olive baboons can be said to reconcile 'implicitly' - they do not appear to use any special conciliatory signals (de Waal & Ren 1988).

The nature and context of the conflict

If one of the combatants had been eating or foraging when aggression began, conciliatory tendency was markedly reduced. The extremely low conciliatory tendency associated with conflict around resources echoes the greatly reduced reconciliation rates observed in wild longtailed macaques (Aureli 1992) and wild moor macaques (Matsumura 1996) following conflicts over food. Given that our understanding of reconciliation has been built mainly on the study of captive primates, this

result merits emphasis, because in contrast to the captive situation foraging occupies the greater part of the activity budget of wild baboons, as is the case for most free-ranging primates (Clutton-Brock 1977; Oates 1987). Aureli (1992) argues that conflicts over food may not disturb the social relationship between individuals: dominance is 'about' access to resources, therefore food conflicts may not be as socially disruptive, and thus as stressful, to victims as other conflicts because a clear infringement of a dominant's claim to priority of access has been made and 'punished'. If conflicts over food do not disrupt relationships and/or produce less stress, then reconciliation will not be important either functionally or proximately in this context. However, in this population we found no evidence that food conflicts were followed by significantly lower rates of combatant self-directed behaviour, an index of stress, than conflicts without an obvious context (Castles & Whiten in press b).

Aureli (1992) also offers an alternative explanation. Because the brief time window in which reconciliation normally occurs is often filled by foraging behaviour (and presumably is even more likely to be so after food conflicts) opponents may be simply diverted from reconciling. It is possible that reconciliation is delayed in such situations but, since most PCs were of 15 minutes duration, this does not appear to be the case here. Furthermore, experimentally induced food conflicts among juvenile rhesus macaques were not reconciled at any stage of a 30 minute sample, even though all food was consumed within the first 10 minutes of samples (de Waal 1984).

Among females, conflicts in which at least one participant was carrying a dependent infant were particularly likely to be reconciled. This result parallels Seyfarth's (1976) observation that post-conflict affiliation was more frequent between adult female chacma baboons when one of the combatants was lactating, and increased reconciliation by female chacmas with the mothers of young infants (Silk et al. 1996). As these authors point out, female baboons are highly attracted to young infants (e.g. Altmann 1980) and thus the social value of mothers of young infants will be raised,

supporting the hypothesis that higher reconciliation rates should occur following conflicts with valuable partners.

While the context of aggression markedly altered the likelihood of reconciliation, the nature of the aggression per se had no discernible effect: low intensity conflicts were as often reconciled as those of a higher intensity, while neither the decidedness of a conflict nor its directionality affected reconciliation rate. These findings contrast with the suggestion that reconciliation should be favoured where dominance asymmetries are weak: that species with high levels of bidirectional conflicts should show high conciliatory tendency and that individual bidirectional and undecided conflicts should be more frequently reconciled (Thierry 1990a; Petit & Thierry 1994a, b). In this population, almost a quarter of sampled conflicts involved retaliation but these conflicts were not more frequently reconciled and overall conciliatory tendency was not particularly high. Though higher rates of reconciliation were reported following undecided, bidirectional conflicts among longtailed macaques (Aureli et al. 1989), such conflicts were relatively rare events. Thus, the critical factor may be whether bidirectional and undecided conflicts leave opponents more stressed and uncertain than unidirectional, decided conflicts and since bidirectional conflicts are relatively common in this population, there may be no increased proximate incentive to reconcile. Data on baboon self-directed behaviour supports this suggestion (Castles & Whiten in press b), while Petit & Thierry (1994b) saw no increase in conciliatory tendency following bidirectional conflicts in a group of captive Guinea baboons (*P. papio*) which also exhibited frequent retaliation.

The nature of the opponents

For olive baboons, it appears that the relative age and sex of individuals involved in conflicts is not an important determinant of whether reconciliation will occur or not. This could be because the relatively low conciliatory tendency of the species made differentiation of classes harder.

Alternatively, it can be seen as support for Byrne et al.'s (1987) suggestion that among baboons, relationships between the sexes are at least as important to individuals as those within them. If relationship quality is an important determinant of conciliatory behaviour then it seems that these baboons do not develop strong or weak relationships exclusively with one sex or age group. Preliminary evidence for the importance of relationship quality is that closely related animals were considerably more likely to reconcile conflicts than other individuals. However, kinship is just one dimension of relationship quality; rank distance is a more indirect measure of relationship quality which also captures effects of extended kin networks, few of which were known in this troop. Rank distance affected reconciliation frequency: individuals who were closer in rank reconciling more often than those who were further apart in the dominance hierarchy and whom we would expect to have weaker relationships.

Post-conflict affiliation with others

In contrast with chimpanzees and in common with other cercopithecine primates (de Waal & Aureli 1996), baboons, whether they were victims or aggressors, were not any more likely to be involved in affiliation with non-combatants following conflicts. Furthermore, unlike longtailed macaques (Aureli et al. 1991a), there was no evidence that victims of aggression increased attempts to initiate affiliation with others. Indeed, for both aggressors and victims, affiliative initiative was more or less equally shared with bystanders in both the PC and the MC. Similarly, though kin might be considered the most likely candidates for consolatory behaviour, baboons were not involved in more affiliative interactions with their close kin in PCs than in MCs.

Combatants did more frequently affiliate with the kin of their former opponent following aggression. Similar behaviour in other monkeys has been labelled 'substitute reconciliation' implying that former opponents can attempt an indirect restoration of their relationship via each other's kin. In

studies which distinguished between victims and aggressors, only increased affiliation between aggressors and the victim's kin has been quantitatively demonstrated (Judge 1991). In this study, both aggressors and victims increase affiliation with their opponent's kin, though interactions with victims were predominantly the responsibility of the aggressor's kin. Furthermore, affiliation with the opponent's kin was an infrequent event and the statistical increase in the PCs is mainly attributable to the paucity of MC interactions with opponent's kin.

How these results bear upon de Waal and Aureli's (1996) social cognition and social constraints hypotheses is not entirely clear. Baboons have high proportions of neocortex relative to other cercopithecine primates (Dunbar 1992) but there is little sign of the 'theory of mind' attributed to chimpanzees (Whiten 1996). If de Waal and Aureli (1996) are correct in linking consolation with empathy as one aspect of such an ability, then baboons would not be expected to console visibly stressed conspecifics. Social constraints, on the other hand, are perhaps not as marked in this species as in some macaques. Redirection of aggression is rare, but the lack of redirection does not imply that there is no risk of receiving aggression for a potential consoler: absence of redirection and of consolation could both be produced by a desire on the part of uninvolved bystanders not to place themselves in dangerous situations. If there are dangers involved in approaching former combatants, we would expect these to vary according to the relative fighting abilities of the potential affiliate and the original combatants such that individuals of high fighting ability will be at lesser risk. This is borne out by the behaviour of mature males who are keen to support mature females in conflicts and then affiliate with them. However, there are obvious potential benefits to males of supporting, buffering and affiliating with females with regard to the inception and strengthening of male-female friendships (Smuts 1985; Strum 1987, 1995). On the whole then, the evidence tends toward supporting the social cognition hypothesis, especially as bystanders do not appear to actively avoid affiliation with former

combatants (PC and MC affiliation with others occurs equally often) as we might expect if such behaviour was costly.

Redirected aggression

Baboons who received aggression did not redirect aggression to uninvolved individuals any more often than they attacked individuals in MCs. Numerous studies of captive macaques have documented the tactic of rapidly redirecting aggression to third parties, but the phenomenon is not restricted to captive animals: Aureli (1992) found very similar rates of redirection in wild and captive longtailed macaques. However, the longtailed macaques of Ketambe frequently feed on clumped food sources, such that recipients of aggression will have more potential targets nearby to redirect to than do the olive baboons at Chololo, who mostly forage in a spatially dispersed pattern (Barton 1993; Barton & Whiten 1993; Barton et al. 1996). Additionally, olive baboon aggression is less unidirectional than longtailed aggression and the more sexually dimorphic males often become involved in male-female and female-female aggression. The first factor may reduce the necessity of redirecting aggression while both factors may increase the costs of redirecting: individuals may have to choose targets carefully to avoid receiving further aggression. Data from wild mountain gorillas provide some support for this suggestion: females, who are often involved in bidirectional contests, rarely redirected received aggression; subordinate males, who rarely retaliate, redirected aggression from dominant males to adult females, but generally did this out of sight of the dominant male (Watts 1995b).

Ethology, **in press**.

Chapter 5. POST-CONFLICT BEHAVIOUR OF WILD OLIVE BABOONS. II. STRESS AND SELF-DIRECTED BEHAVIOUR

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Abstract

Previous studies indicate that the proximate function of post-conflict affiliative interaction among primates is to reduce victims' uncertainty about their opponent's future behaviour: the 'uncertainty reduction hypothesis' (Aureli & van Schaik, 1991, Ethology, 89, 101-114). This study confirms and extends these results demonstrating that they are neither a product of captivity nor specific to macaques: both victims and initiators of aggression in a large group of wild olive baboons exhibited elevated rates of self-directed behaviour (SDB) - scratching, autogrooming, body-shaking and yawning - in a 10 minute post-conflict period. During this period they were more likely to receive further aggression. Reconciliation reduced both SDB and the incidence of further aggression. However, reconciliation only reduced SDB among individuals involved in conflicts in which they had both received and delivered aggression. It is suggested that aggressors in unilateral conflicts were aroused rather than uncertain and that their victims' lack of control over post-conflict interactions (which tended to be initiated by their opponents) prevented them from benefiting from reconciliation in the same fashion as longtailed macaque victims, who frequently initiated reconciliation.

Introduction

The 'stress response' is an adaptive mechanism which physiologically prepares animals to respond to dangerous situations (e.g. Sapolsky 1994). Adrenal hormones rapidly mobilise stored energy and increase heart rate, blood pressure and breathing rate to allow this energy to be utilised. In addition, energy storage, growth, immune system and reproductive processes are inhibited. Sustained activation of the stress response is associated with a range of deleterious consequences including brain damage (Uno et al. 1989), retarded growth (Denenberg & Karas 1959, 1961), immunodeficiency (Kaplan et al. 1991b) and reproductive suppression (Wasser & Barash 1983; Sapolsky 1986). In socially competitive environments, fellow group members are potential stressors (e.g. Dunbar 1988) and chronic social stress can result in severe circulatory disorder and death in captive primates (Kaplan et al. 1991a). Chronic social stress is more likely to occur in environments in which it is impossible or particularly costly for stressed individuals to leave the group. Therefore, animals which form groups in response to predation pressure and are thus frequently exposed to social stress are expected to develop social mechanisms for attenuating its potentially destructive effects (Aureli et al. 1991).

Among non-human primates, displacement, or self-directed, behaviours (SDB), such as scratching, autogrooming and yawning, are most common in stressful situations (Maestripieri et al. 1992). For example, rhesus macaque, *Macaca mulatta*, mothers scratched at higher rates when their infants moved away from them and when their infants came into proximity with individuals who regularly harassed them (Maestripieri 1993). In female long-tailed macaques, *M. fascicularis*, autogrooming is most frequent when within 1 m of the alpha male (Troisi & Schino 1987), and the delayed establishment of dominance relationships between unfamiliar female pairs results in marked increases in scratching, autogrooming and yawning (Schino et al. 1990). Pharmacological evidence supports the link

between SDB and anxiety, with anxiogenic drugs increasing and anxiolytic drugs reducing SDB expression (Ninan et al. 1982; Insel et al. 1984; Schino et al. 1991). Thus, SDB appears to have considerable promise as a behavioural measure of anxiety in non-human primates.

By employing measures of SDB in such a fashion, studies of captive longtailed macaques demonstrate that victims of aggression experience elevated levels of stress in the immediate post-conflict period (Aureli et al. 1989; Aureli & van Schaik 1991b; Aureli in press). In addition, Aureli and co-authors found that affiliative interactions between victims and their former opponents soon after the conclusion of their conflict (i.e. reconciliation: de Waal & van Roosmalen 1979) reduced victims' stress to the level of non-conflict periods, while Smucny et al. (1996) report that aggression increases, and reconciliation reduces, heart rate in rhesus macaques. Underpinning this work is the Uncertainty Reduction hypothesis (Aureli & van Schaik 1991b): that following conflicts, victims are stressed because they are uncertain as to the future behaviour of their opponent and other group members, from whom they are likely to receive further aggression, and their uncertainty and stress is manifest in increased rates of SDB. Reconciliation reduces the risk of receiving further aggression, reducing victims' uncertainty. Therefore, the proximate cause of reconciliation lies in its ability to reduce uncertainty, alleviating stress. It should be noted that the potential benefit of reconciliation in reducing stress can, initially, lead to increased uncertainty: reconciliation requires close proximity to the opponent, thus victims are likely to experience motivational ambivalence over whether to withdraw from their opponent, to avoid further attack, or to approach in order to reconcile. Once there is an immediate potential benefit to reconciliation - a reduced risk of receiving aggression - the victim's decision to approach or withdraw from its opponent becomes harder, the victim should experience increased uncertainty and be in more need of reconciliation; i.e. the stress reduction function may be self-reinforcing.

Recently, evidence that in Barbary macaques, *M. sylvanus,* and longtailed macaques, aggressors and victims alike exhibit increased levels of SDB in the post-conflict period (Aureli in press; Das et al. submitted), has led to an extension of the hypothesis. Aureli suggests that both the aggressor and the victim are uncertain about their opponent's future behaviour because their relationship is at risk and that reconciliation, by repairing the relationship (e.g. Castles et al. 1996), also serves to reduce this source of uncertainty.

While plausible, these explanations are based upon work on just three captive populations of macaque. It is possible that the post-conflict stress experienced by captive macaques is either a) a phenomenon restricted to the genus *Macaca*, or b) a product of the captive environment, or both. Before accepting uncertainty reduction as a general explanation of primate post-conflict behaviour, the effects upon which the hypothesis is based should be replicated in other taxa and in free-ranging populations. Two papers take steps in this direction. First, Aureli (1992) demonstrated that free-ranging longtailed macaque victims had higher rates of scratching and were more likely to receive further aggression in the post-conflict period. Second, in an experimental study of free-ranging chacma baboons, *Papio ursinus*, Cheney et al. (1995) played back a potentially threatening scream of a former aggressor to its recent victim. Victims looked towards the location of such screams for a shorter period of time when they were played back soon after their former opponent had approached them while grunting than they did when there had been no post-conflict interaction with the former opponent. The authors interpret this reduced responsiveness as a sign that the relationship between the victim and the aggressor had been restored to baseline tolerance levels. However, the authors present no direct measure of tolerance and a more parsimonious interpretation is that victims were simply less alert to their former opponent's screams following affiliative interaction. So, while victims were less alert to one potential source of danger and possibly less uncertain as to their former aggressor's future

behaviour, it is not clear that they were less stressed as no behavioural or physiological measures of anxiety were recorded. Furthermore, the study was of restricted scope, being limited to adult female victims and one form of 'reconciliation' which was always initiated by aggressors.

The aim of this study is to test and extend the uncertainty reduction hypothesis by examining the post-conflict behaviour of a population of wild olive baboons, *P. anubis*. To this end we examine the effect of aggression upon the SDB of victims and aggressors (both male and female), and the effect of reconciliation on former combatants' SDB rates. We predict that rates of SDB and received aggression will be elevated above baseline levels following conflicts, and that reconciliation will significantly reduce both aggression and SDB rates.

Methods

Details of the site and subjects of this study and data collection can be found in Castles & Whiten (in press a). In addition, post-conflict (PC) and matched control (MC) data on self-directed behaviour were recorded continuously. Definitions follow Schino et al. (1988):

Scratch - (usually repeated) movement of the hand or foot during which the digits are drawn across the fur or skin.

Self-groom & self-touching - picking through and/or slowly brushing aside fur with one or both hands. Brief self-touching included wiping eyes, inspecting feet and placing hand to mouth.

Body-shake - shaking movement of entire body (similar to that of a wet dog).

Yawn - brief gaping movement of the mouth. Not recorded as a SDB if accompanied by aggressive signals such as eye-flash or canine-whetting.

Scratching and self-grooming were scored as bouts of undefined duration. A break of at least 5 seconds, or a switch to another class of SDB, was required before scoring a new bout. Yawn and body-shake were scored on each occurrence.

Analysis

A total of 454 PC and MC observations were collected on 56 different focal subjects (mean = 8.1 per focal subject; range = 1 - 22). For the purpose of these analyses, reconciliation was said to occur if the focal animal was involved in an affiliative interaction with a former opponent at any point within the first 10 minutes of the PC. Reconciliation occurred in 80 PC-MC pairs.

Analyses are based on a method developed by Aureli & van Schaik (1991b). First, we calculated the temporal distribution of self-directed behaviours during the first 10 min of PCs in which focal individuals neither reconciled nor were involved in aggressive interactions (these were excluded because such post-conflict events were expected to affect SDB rate). Because SDB activities are relatively rare, individuals' mean scores for each minute of each PC and MC would be unreliable, so the PC distributions were derived by dividing the total number of a given class of PC SDB bouts (e.g. yawns) by the total number of PCs without reconciliation or further aggression (N=302). Next, we calculated individuals' mean rate of each class of SDB (in bouts per min) over the first 10 min of the MCs (mean values were used because no significant deviation from a flat time course distribution was either expected or found in the MCs). Then, we derived the 95% confidence intervals of individuals' MC SDB rates and used these as a baseline with which to compare the rate in each consecutive minute of SDBs in the PCs. Finally, we checked that the extreme behaviour of a few individuals was not responsible for PC values differing from those in the MC (and that PC distributions were significantly different from MC distributions)

by running Wilcoxon signed ranks tests on individual focal animals' mean PC and MC SDB rates.

The second stage of the analyses concerned the effect of reconciliation on SDB and involved a comparison of SDB frequency in the PCs in which reconciliation did not occur with that in PCs with reconciliation. Here, the rarity of reconciliation exacerbates the problem of attaining precise measures of SDB rate. Therefore, we combined all SDB measures and derived a time window in which the combined PC SDB rate deviated from the 95% confidence interval of the combined MC SDB rate. We then compared the rate of individuals' SDB following reconciliation within this time window to that in PCs without reconciliation.

Analyses were one-tailed when we had specific predictions from previous studies and two-tailed elsewhere. The significance level was 5%.

Results

The effect of conflict on self-directed behaviour

After conflicts baboons increased their rate of all four categories of self-directed behaviour in those PCs in which no reconciliation or further aggression occurred. Rates were increased above the 95% confidence interval of the MC mean as follows: for scratching, during the first min and between the fifth and ninth min after conflict had ended (Fig. 1); for self-grooming, for the first 5 min and again in the seventh min (Fig. 2); for body-shake, for the initial 4 min, the sixth min and again from the eighth min (Fig. 3); and yawning rates were above control levels for the initial 4 min and between the sixth and eighth min (Fig. 4).

These effects were not the product of aberrant behaviour from a few individuals: Using Wilcoxon signed ranks tests, we compared individuals' mean PC and MC rates for the first 10 min of each observation period (for the 39 animals with at least 3 qualifying PCs: scratching: $z=4.87$, one-tailed $p<0.001$; self-groom: $z=4.99$; one-tailed $p<0.001$; body-shake: $z=2.58$, one-tailed $p<0.005$; yawn: $z=2.14$, one-tailed $p<0.05$).

Figure 1

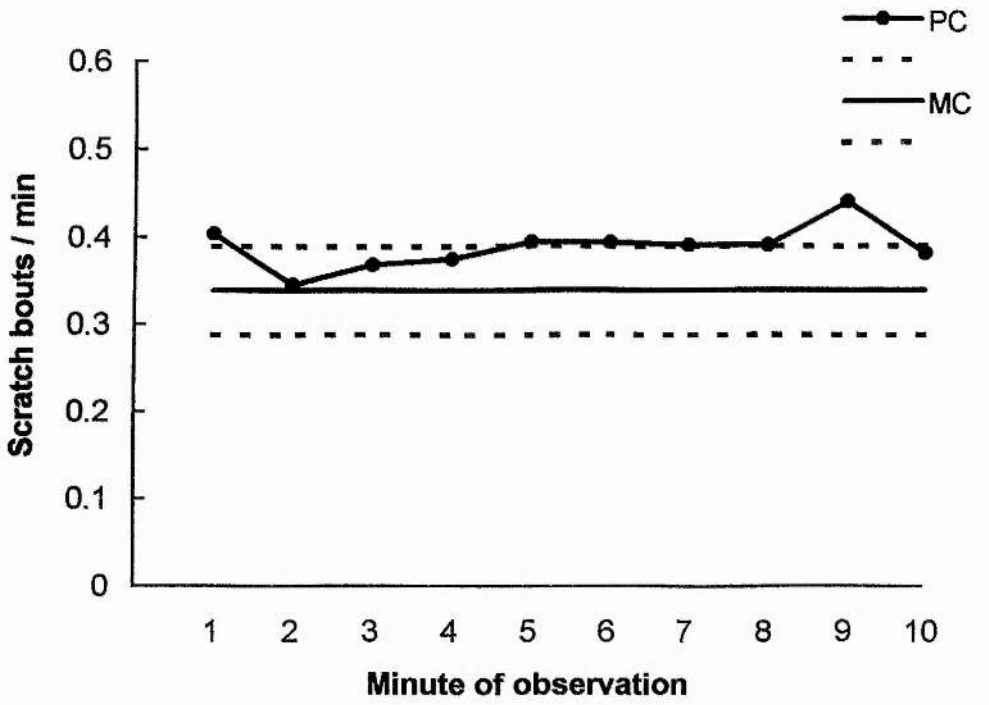

Figure 1. Scratch rates per min during post-conflict (PC) observations without reconciliation or further aggressive interactions and matched control (MC) observations. The PC distribution is the mean for each min, the MC distributions, the mean plus the 95% confidence limits of individual averages over the first 10 mins.

Figure 2

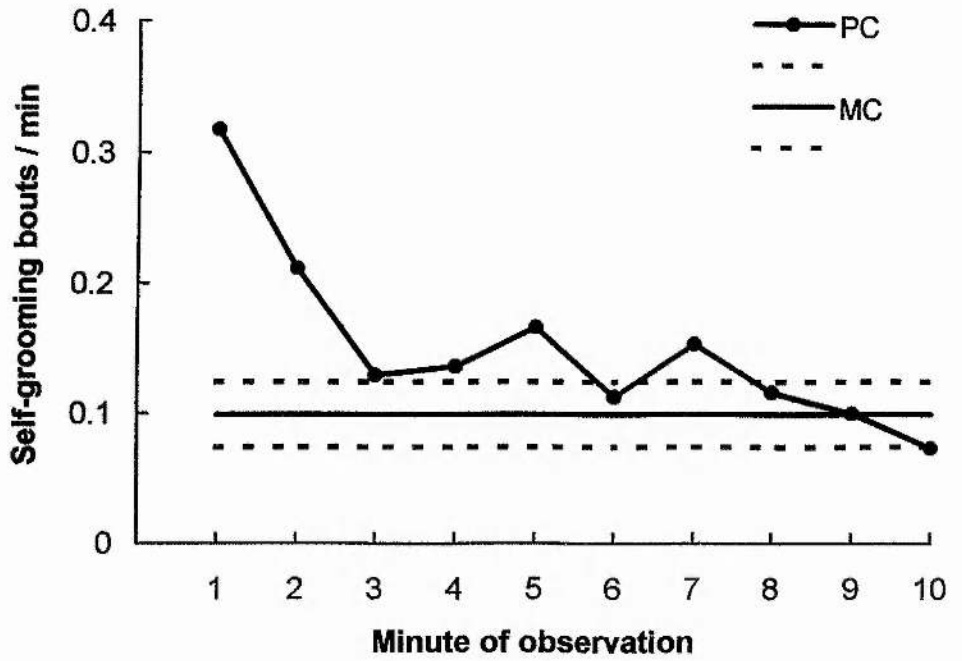

Figure 2. Self-grooming rates per min during post-conflict (PC) observations without reconciliation or further aggressive interactions and matched control (MC) observations. The PC distribution is the mean for each min, the MC distributions, the mean plus the 95% confidence limits of individual averages over the first 10 mins.

Figure 3

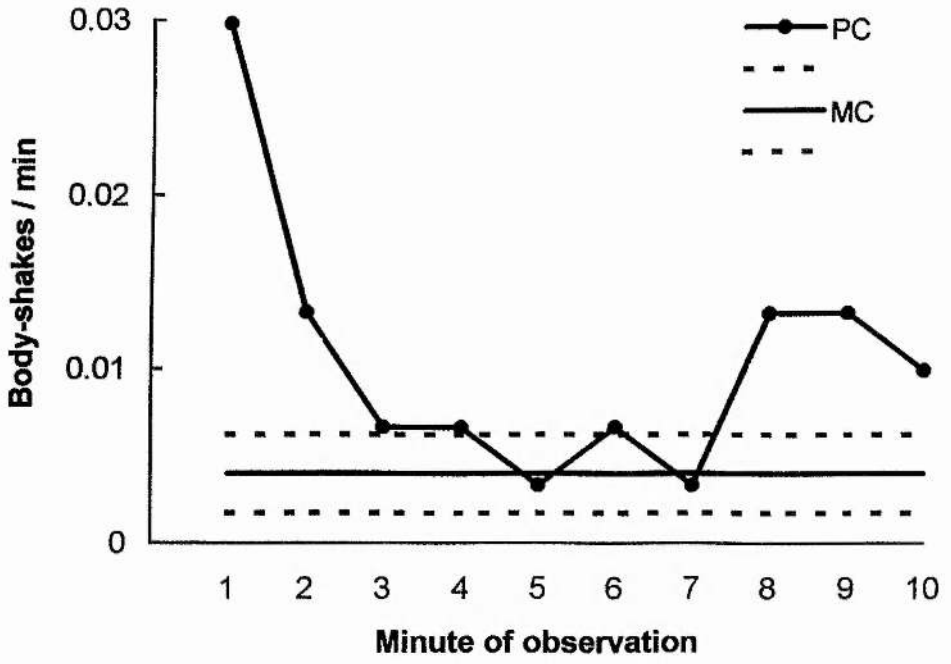

Figure 3. Body-shake rates per min during post-conflict (PC) observations without reconciliation or further aggressive interactions and matched control (MC) observations. The PC distribution is the mean for each min, the MC distributions, the mean plus the 95% confidence limits of individual averages over the first 10 mins.

Figure 4

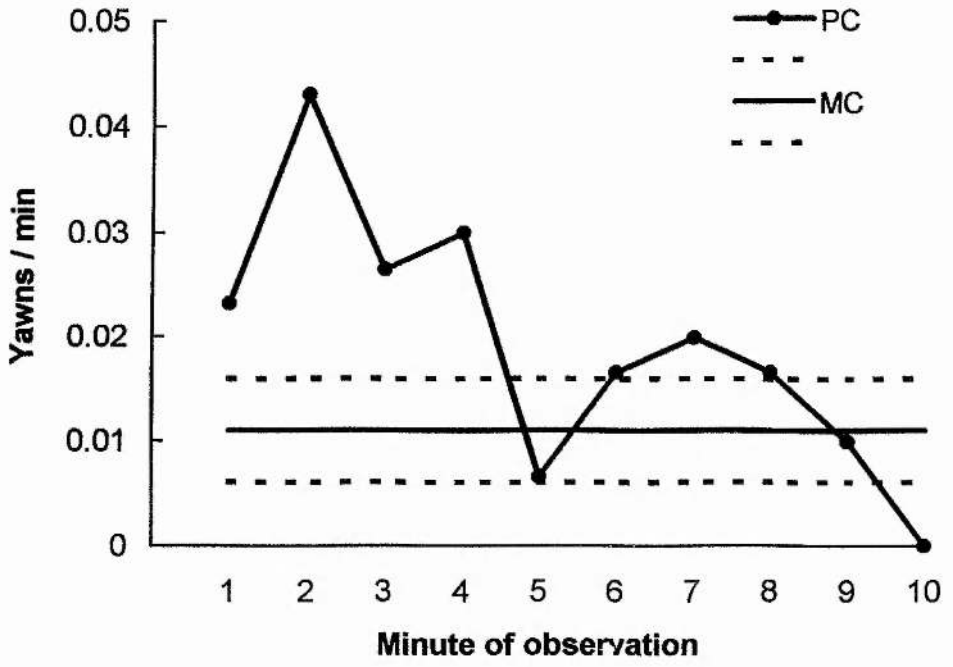

Figure 4. Yawn rates per min during post-conflict (PC) observations without reconciliation or further aggressive interactions and matched control (MC) observations. The PC distribution is the mean for each min, the MC distributions, the mean plus the 95% confidence limits of individual averages over the first 10 mins.

As all four classes of SDB increased in frequency following unreconciled conflicts, further analyses concern a combined SDB measure in which the four categories are summed to produce an overall rate of SDB bouts per min. This overall SDB rate is above control levels until the 9th min of PCs (Fig. 5) and the elevation is representative of individual PC and MC frequencies (Wilcoxon signed ranks test: N=39, z=4.44, one-tailed $p<0.001$).

The effect of reconciliation on self-directed behaviour

For baboons that reconciled, we compared SDB rates following reconciliation to those in unreconciled PCs. Because SDB rate was very high in the first few minutes of unreconciled PCs (Fig. 5) and the average latency to reconciliation was 160 s we did not compare SDB rate during the entire 9 min time window. Instead, in the reconciled PCs, we derived the SDB rate in the portion of the 9 min subsequent to reconciliation, while in the PCs without reconciliation we calculated SDB rate after discarding events which took place before the average latency time to reconciliation (i.e. from the beginning of the 4th until the end of the 9th min). As Figure 6 indicates, there were significantly fewer bouts of SDB following reconciliation than in unreconciled PCs (Wilcoxon signed ranks test: N=34, z=2.71, one-tailed $p<0.005$) while the mean post-reconciliation SDB rate (0.42 bouts / min) fell to within MC confidence limits. Furthermore, in the 80 reconciled PCs, baboons' SDB rates prior to reconciliation were both above those in the MC (Wilcoxon signed ranks test: N=36, z=2.92, one-tailed $p<0.005$) and significantly higher than their SDB rates following reconciliation (N=36, z=2.45, one-tailed $p<0.01$; note that this result is expected purely from the time course of post-conflict SDB). These results demonstrate that reconciliation reduced the frequency of a behavioural index of stress.

The nature and context of the conflict

Focal animals exhibited similar, elevated rates of SDB in the 9 min periods following unreconciled high intensity conflicts (chases, grappling, biting and

Figure 5

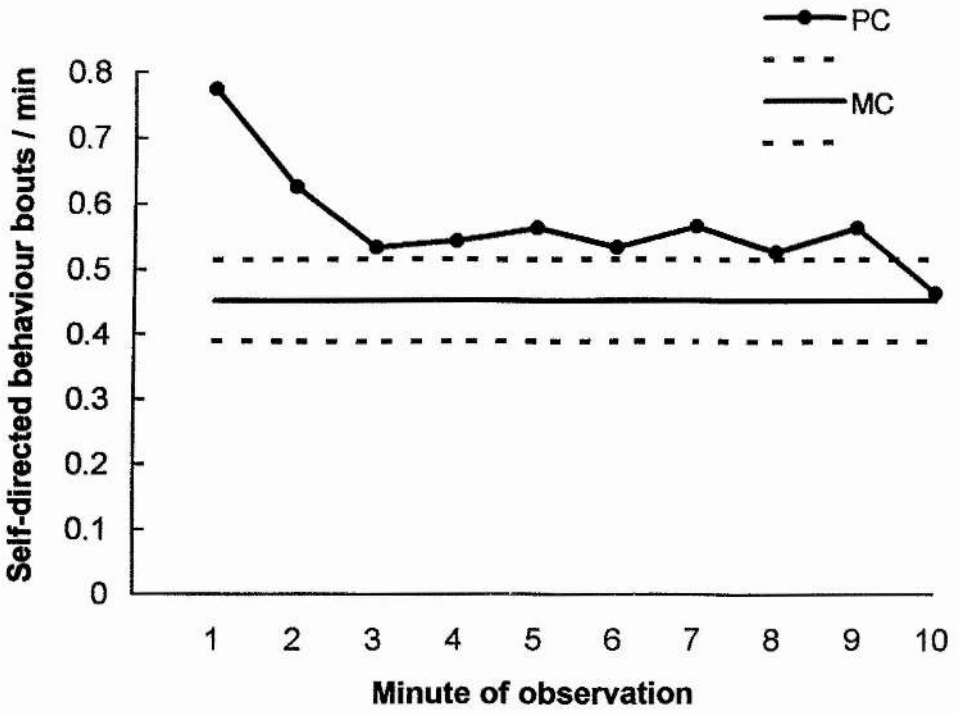

Figure 5. Combined self-directed behaviour (scratch + self-groom + body-shake + yawn) rates per min during post-conflict (PC) observations without reconciliation or further aggressive interactions and matched control (MC) observations. The PC distribution is the mean for each min, the MC distributions, the mean plus the 95% confidence limits of individual averages over the first 10 mins.

Figure 6

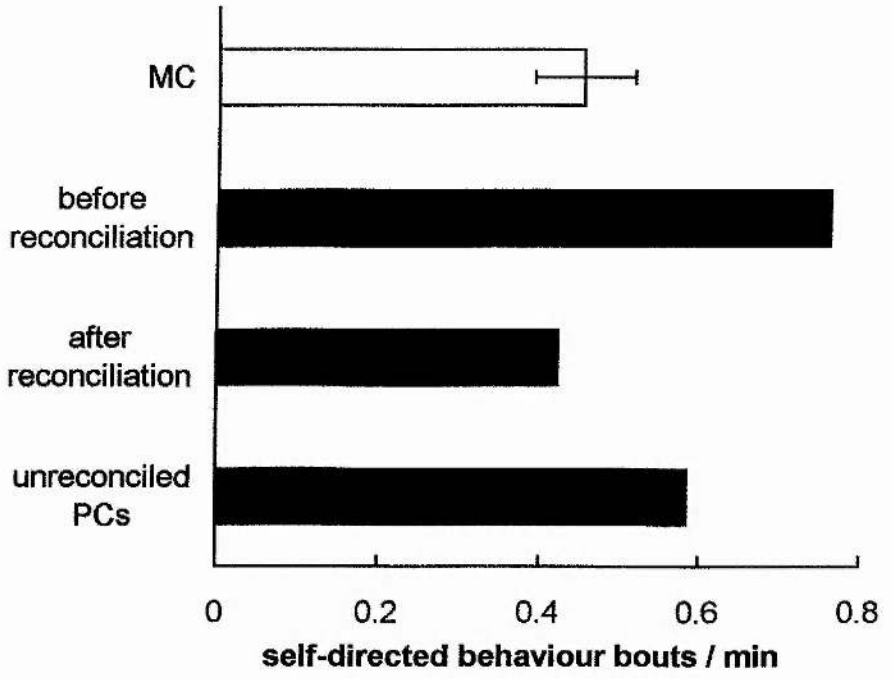

Figure 6. Self-directed behaviour rates during post-conflict (PC) periods. Rates for unreconciled PCs are for the 4th to 9th min. Rates before and after reconciliation represent the proportion of the 10 min period prior to and following the first conciliatory interaction. The matched control (MC) observation rate is the mean and the 95% confidence limit of individual averages over the first 10 min.

bi-directional conflicts; mean=0.6 bouts / min) and unreconciled low intensity conflicts (threats and lunges: 0.53 bouts / min; Wilcoxon signed ranks test: N=34, z=1.56, two-tailed p>0.1). For both intensities SDB rates for unreconciled conflicts were above baseline levels (high intensity: N=39, z=3.85, p<0.001; low intensity: N=21, z=2.38, p<0.01; for individuals with at least 2 qualifying PCs).

Likewise, the context of aggression did not appear to affect SDB rates in unreconciled PCs: SDB rates following conflicts over food were similar to those when their was no obvious context to aggression (mean=0.53 vs. 0.62 bouts / min; Wilcoxon signed ranks test: N=33, z=0.96, two-tailed p>0.3). In both contexts unreconciled PC SDB rates were above MC levels (food: N=21, z=2.45, p<0.01; no context: N=39, z=3.22, p<0.001; for individuals with at least 2 qualifying PCs).

Victims and aggressors

To determine whether post-conflict increases in SDB rate were common to both aggressors and victims we examined individuals' SDB following conflicts in which they had been either unilateral aggressors (animals who initiated a dyadic or all polyadic conflicts preceding a PC in which no counter-aggression was received) or unilateral victims (animals who received aggression without retaliating or initiating a further conflict prior to the PC). We also examined the behaviour of individuals when they were neither unilateral aggressors nor unilateral victims (animals in dyadic conflicts which involved counter-aggression or polyadic conflicts in which they initiated and received aggression). There were 115 aggressor, 109 victim and 78 bidirectional PCs in which there was no reconciliation or further aggression. In all three data sets, PC SDB rate was above control levels (Fig. 7), and this effect was not due to the extreme behaviour of a few individuals (Wilcoxon signed ranks test: aggressors: N=37, z=3.41, p<0.001; victims: N=35, z=2.27, p<0.05; bidirectional: N=36, z=2.54, p<0.01).

Figure 7

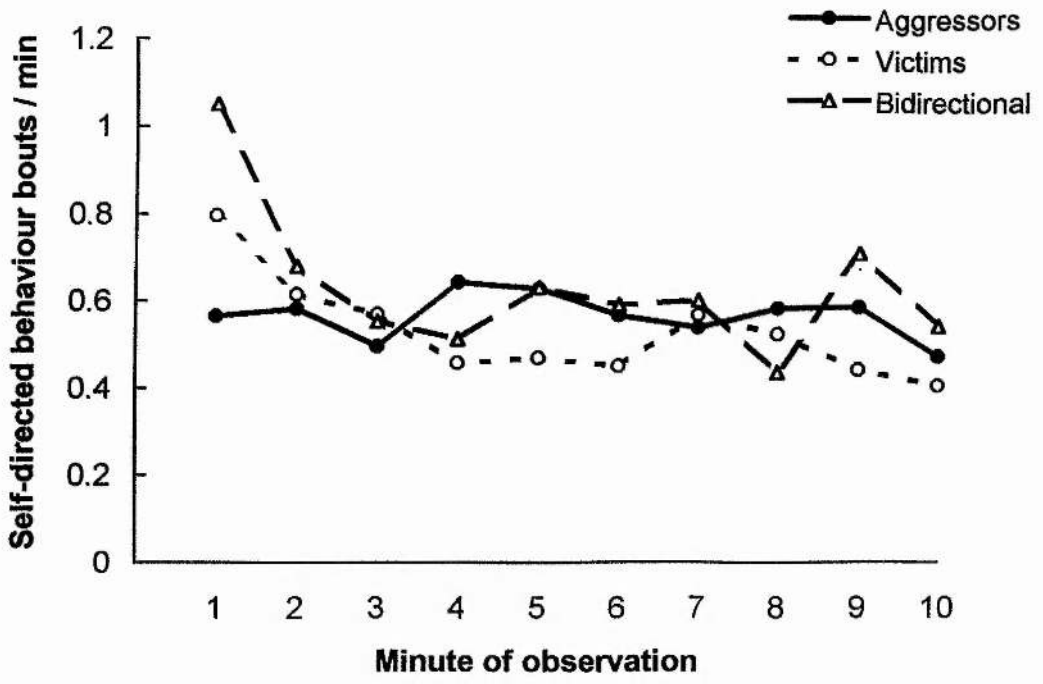

Figure 7. Self-directed behaviour rates per min for unilateral aggressors, unilateral victims, and bilateral opponents during the first 10 min of post-conflict (PC) observations without reconciliation or further aggressive interactions.

Although the time course of the SDB response appears to be slightly different for unilateral aggressors, victims and others, there was no significant difference in mean SDB rate over the 10 min PC period for individuals sampled in all three classes (aggressors: 0.57 bouts / min, victims: 0.53, bidirectional: 0.62; Friedman 2-way ANOVA: N=19, χ^2=2.39, df=2, p>0.3).

Formal testing of the effect of reconciliation on SDB rates separated for victims, aggressors and bidirectional conflicts is problematic because of the limited sample sizes, but SDB frequency was significantly reduced following reconciliation in bidirectional PCs relative to rates before reconciliation (29 reconciled pairs: 0.34 vs. 0.94 bouts / min; Wilcoxon signed ranks test: N=18, z=2.63, one-tailed p<0.005) and in unreconciled PCs from the 4th until the 9th min (0.31 vs. 0.57; N=14, z=1.79, one-tailed p<0.05). There were no significant reductions in the mean SDB rates following reconciliation relative to unreconciled PC rates for unilateral aggressors (24 pairs: 0.52 vs. 0.55) and unilateral victims (25 pairs: 0.67 vs. 0.54).

Females and males

We tested whether aggression had a comparable effect on both females and males by analysing their behaviour separately. The time course of SDB bouts was similar for both sexes, being above baseline levels for the first 9 min for females and the first 7 min and the ninth min for males. These increases were apparent in most individuals with 3 or more PCs (females: 0.56 vs. 0.40 bouts / min; Wilcoxon signed ranks test: N=22, z=3.36, p<0.001; males: 0.65 vs. 0.43; N=17, z=2.86, p<0.005). The increases remained when juveniles were excluded (females: 0.54 vs. 0.40: N=16, z=2.79, p<0.005; males: 0.62 vs. 0.42; N=13, z=2.27, p<0.05).

For females, SDB rates following reconciliation were lower than those from the 4th until the 9th min of unreconciled PCs (0.38 vs. 0.52 bouts / min; Wilcoxon signed ranks test: N=23, z=2.06, p<0.05). Male post-reconciliation

SDB rates were not significantly lower (0.47 vs. 0.73; N=11, z=1.50, p>0.1), although this may be due to the limited sample size: there were just 23 PCs in which a male focal animal reconciled.

Further Aggression

The majority of combatants, whether victim or aggressor, display increased levels of post-conflict stress. This stress response should leave them physiologically prepared for further aggression. Indeed, former combatants are more likely to be involved in further aggressive interactions (with former opponents and other baboons) in the PC period. We calculated the baseline rate and 95% confidence intervals of MC aggressive interactions from individuals' mean rates (the first 10 min were combined as we expected, and found, no time course pattern in this condition). Then, we plotted the rate of aggressive interaction in PCs without reconciliation in each of the first 10 minutes (Fig. 8). The rate for PCs is higher than the MC upper confidence limit for the majority of the observation period, and this effect was replicable at the individual level (mean=0.026 vs. 0.013 bouts / min; Wilcoxon signed ranks test: N=55, z=2.89, one-tailed p<0.005). Following reconciliation baboons were less likely to become involved in aggression than when they were in the first 10 min of unreconciled PCs (0.011 vs. 0.025 bouts / min; Wilcoxon signed ranks test: N=35, z=1.96, one-tailed p<0.05; for unreconciled PCs we discarded events which took place before the average time to reconciliation). Furthermore, the mean rate of aggression following reconciliation fell to within MC confidence limits.

The likelihood of being involved in further aggression was increased relative to control observations for unilateral aggressors (mean=0.018 vs. 0.014) and bidirectional combatants (0.031 vs. 0.014), but only significantly so for unilateral victims (0.030 vs. 0.013; Wilcoxon signed ranks test: N=39, z=1.80, one-tailed p<0.05).

In the post-conflict period, baboons were particularly likely to be the recipients of further aggression. Mean rates of received aggression in the

Figure 8

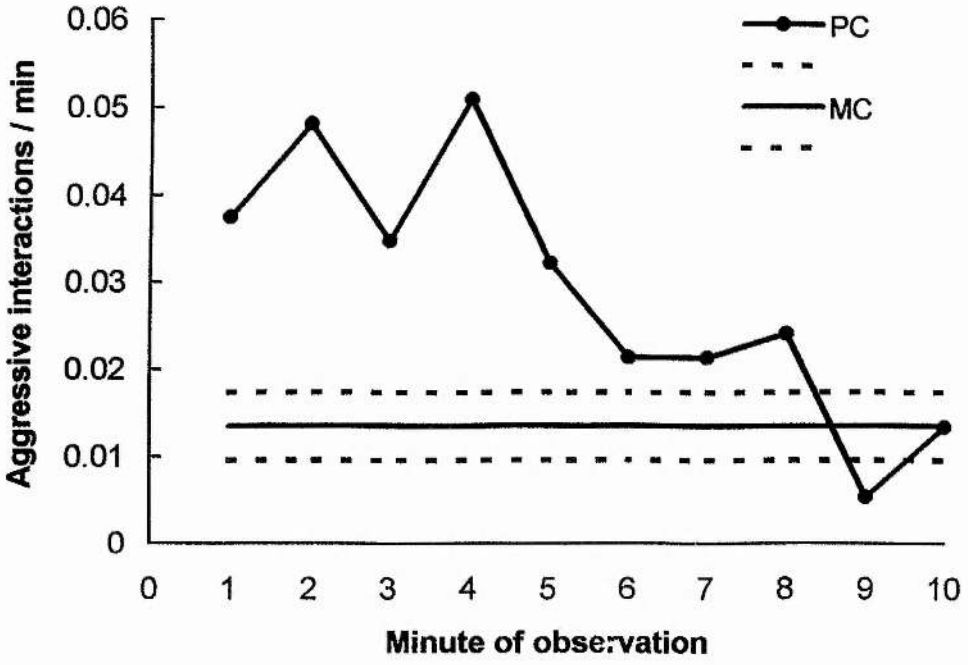

Figure 8. Rates of aggressive interaction during post-conflict (PC) obseravtions without reconciliation. The matched control (MC) observation rate is the mean and the 95% confidence limit of individual averages over the first 10 min.

PCs were higher than those for MCs (0.016 vs. 0.007; Wilcoxon signed ranks test: N=55, z=2.67, one-tailed p<0.005). Mean rates of received aggression following reconciliation (0.006) were lower than those in unreconciled PCs (0.017; N=35, z=1.88, one-tailed p<0.05; for unreconciled PCs events prior to the average latency time to reconciliation were discarded). Prior to reconciliation the mean rate of received aggression (0.018) was above baseline levels while after reconciliation the frequency (0.006) dropped to within MC confidence limits.

Increases in receipt of aggression in unreconciled PCs relative to MCs could be statistically demonstrated for unilateral victims only: (0.020 vs. 0.008; Wilcoxon signed ranks test: N=39, z=2.21, one-tailed p<0.05). Bidirectional combatants' mean PC rate was higher (0.016 vs. 0.007), while aggressors received similar levels of aggression in both conditions (0.005 vs. 0.006).

Discussion

Wild olive baboons suffered a clear stress response in the period following a conflict, indexed, in this case, by elevated rates of scratching, autogrooming, yawning and body-shaking. This increase was common to all combatants, regardless of sex or their role in the initial conflict. Neither the intensity nor the context of the conflict significantly affected this response. When former opponents interacted affiliatively in the first few minutes of the post-conflict period, their rate of SDB decreased to a level similar to periods without aggression. Reconciliation also reduced the likelihood of becoming involved in further aggression with former opponents and/or other troop members.

The results of this study mirror and extend the findings of work on captive macaques (Aureli et al. 1989; Aureli & van Schaik 1991b; Aureli in press; Smucny et al. 1996; Das et al. submitted). In common with these studies, olive baboon combatants experience stress in the post-conflict period. When opponents reconcile, the risk of further aggression declines to baseline levels as does the rate of SDB. Combatants appear to be calmed

by the process of reconciliation; the stress response is deactivated more rapidly and uncertainty is reduced, confirming the hypothesis of Aureli and van Schaik.

That the effects of aggression and reconciliation upon stress response seem to be similar in captive macaques and free-ranging baboons is important. Previously, it could be argued that post-conflict stress and its alleviation through reconciliation in captivity were artifacts of enforced close proximity: after conflict, combatants cannot place any great distance between themselves and other group members and aggression is likely to recur, so combatants are stressed and uncertain unless they reconcile. However, the Laikipia baboons are not so constrained - while it appears to be risky to leave the group (a former combatant took this option only once in 454 PCs), the group itself is often widely dispersed (Barton 1993; Barton & Whiten 1993; Barton et al. 1996) and combatants can maintain great distance while remaining within the group; yet SDB rates are elevated and aggression is more likely to recur unless opponents reconcile. Therefore, as the work of Aureli (1992) and Cheney et al. (1995) hinted, we can conclude that the stress response costs of aggression and the ability of reconciliation to alleviate them are limited neither to captivity nor to macaques.

However, the picture is less clear when we examine the role of the combatant in the original conflict. The above conclusions are based on data combined irrespective of whether the focal animal only attacked, only received, or both delivered and received aggression during the initial conflict. In terms of the post-conflict stress response, the combatant's role appears to be irrelevant: in all three conditions post-conflict SDB is elevated relative to non-conflict control observations and individuals do not seem to be any more stressed in any one of the roles.

Though Aureli (in press) demonstrates that aggressors and victims exhibit similar post-conflict increases in the frequency of scratching and speculates that reconciliation should lower SDB frequency for both classes of combatants, this is the first study to explicitly address the effect of

reconciliation upon SDB in the aggressive party. The data here are limited, but unilateral aggressors appear to be less or not at all calmed by reconciliation. In fact, with respect to the uncertainty reduction hypothesis, it is unclear why aggressors in this population should show a post-conflict stress response at all as they do not receive higher rates of aggression in this period. Perhaps the answer to this conundrum lies in how we gauged stress: SDB is an intrinsically noisy measure - some of the behaviours recorded are part of normal self-maintenance - so using SDB to measure stress involves separating the stress 'signal' from a relatively high level of noise. While at the physiological level, the post-conflict stress response - the activity of the autonomic nervous system - may be the same whatever the focal's role, for unilateral aggressors, this may be the product of arousal rather than uncertainty. In this case, measuring SDB allows us insight into physiological response but leaves us unclear as to the individual's psychological interpretation of that state. Unilateral aggressors were slightly more likely to initiate aggression in unreconciled PCs. Here, increased levels of SDB may be reflecting activity of the autonomic nervous system which would facilitate further aggression. We would not expect such animals to be anxious about future behaviour if their frequent SDB is a product of being physiologically prepared for action and it is adaptive to remain prepared irrespective of whether they reconcile with their first opponent or not. If this is the case, reconciliation should not reduce SDB rate.

However, for victims the situation is different. In contrast with longtailed macaques, redirecting aggression to others is rarely a viable option in this population (Castles & Whiten in press a), so the stress response mainly prepares victims to receive further aggression from either the original opponent or other conspecifics. The victim is likely to be experiencing uncertainty, unsure of others' intentions. If he or she does reconcile then the chance of becoming involved in more aggression declines to baseline levels; uncertainty has been removed and we should see the expected decline in SDB frequency. In fact, we only see this decline clearly

in animals who are not unilateral victims, i.e. those who fought back during, or redirected the original aggression. This suggests that the uncertainty reduction hypothesis may not be entirely correct. Aureli and co-authors did not partition their data on longtailed macaques according to the victim's aggressive response to the original attack, so we do not know if both unilateral and bidirectional victims benefited from reconciliation in this population.

On the other hand, a critical difference between baboons and longtailed macaques may lie in the victim's role in initiating reconciliation. In longtailed macaques 75% of conciliatory interactions were initiated by victims (Aureli et al. 1989), while in this study, unilateral victims initiated just 38% of such interactions (Castles & Whiten in press a). Control is an important correlate of efficient use of the stress response (Sapolsky 1993), thus the difference between the baboon and macaque populations could be the level of control the victim has over post-conflict interaction with the former opponent. Longtailed macaque victims have more control, as measured by conciliatory initiative, than baboons. This control is exhibited in their choice of conciliatory partners - individuals with whom they share a high quality relationship (Aureli et al. 1989) - who also happen to produce the highest rates of victim SDB (Aureli in press), such that longtailed macaque victims appear to be choosing to reconcile when their stress is greatest. Baboon victims have less control over conciliatory interaction; their opponent tends to initiate. Furthermore, a considerable proportion of unilateral victims who received reconciliation were carrying dependent infants, and the aggressor's approach may have had more to do with achieving access to the infant than restoring its relationship with the opponent. When a unilateral aggressor initiates post-conflict affiliation, particularly when the victim has a young infant, its victim may not be relieved from stress because the best strategy for avoiding further aggression is to permit its opponent to interact with its infant, which is, in itself, stressful (e.g. Maestripieri 1993).

If these differential patterns of post-conflict stress response for unilateral aggressors, victims and bidirectional opponents are representative, then we should question whether the particular class of 'reconciliation' initiated by aggressors toward unilateral victims merits the term, with all of its implications. However, it must be emphasised that our breakdown of reconciled PCs which indicated differential effects of reconciliation on SDB left few PCs in each category of combatant's role, thus these inferences would benefit from further investigation. In particular, special attention should be paid to the interaction between the combatant's role in the initial conflict, post-conflict conciliatory initiative and the stress response.

Chapter 6. SELF-DIRECTED BEHAVIOUR AND THE RELATIONSHIP QUALITY OF WILD OLIVE BABOONS

Introduction

Primate social systems are the products of interactions between individuals (Dunbar 1988; Pusey & Packer 1997). Patterns of interactions can be characterised as relationships, and measures of relationships can be used to characterise and contrast primate societies (Hinde 1979; 1983). Such measures range from the simple, such as measures of aggression and affiliation rate, to the complex (e.g. Drews 1994), making them problematic to apply to differing taxa or ecological conditions.

Simple measures have the advantage of replicability and easy generalisation but, because of this, may lack subtlety. For example, aggression has been utilised as a measure of relationship quality with the assumption that relationships marked by high rates of aggression are of low quality. The reasoning is that aggression carries the costs of being dispersive, stressful and dangerous (Smuts 1987) so individuals will refrain from inflicting such costs on valued social partners. Unfortunately, the validity of this assumption is questionable; at least for cercopithecine primates. If primates invest in those relationships which have the most potential benefit to them (Kummer 1978; Cords & Aureli 1993; Cords 1997) then we would expect the relationships of kin-related animals to be of high quality because related individuals can benefit not just through the exchange of resources or social favours (e.g. de Waal 1989a) but also through the benefits of investing in close relatives fostered by kin selection (Hamilton 1964; see Chapais 1997 for a nepotism threshold in macaques). However, some studies have indicated that rates of aggression are highest among kin (e.g. Japanese macaques: Kurland 1977; vervet monkeys: Horrocks & Hunte 1983; rhesus macaques: Bernstein & Erdhart 1986). This may be because relatives are more often in close proximity and thus have more opportunity to engage in aggression and/or are more likely to come into conflict over, for example, access to resources. Controlling for time in proximity reduces such

disparities but need not necessarily eliminate them. Moreover, it does not relieve the combatants from the costs of engaging in aggression. The aggression still occurs, and it is still dispersive, stressful and potentially injurious. Among cercopithecine primates, it seems that rather than avoiding all aggressive conflict with animals who are of value, individuals selectively alter their behaviour following conflicts and reconcile more frequently (Kappeler & van Schaik 1992; Castles et al. 1996)

A parallel problem exists for positive measures of relationship quality. Elevated rates of active affiliation such as grooming, time spent in contact or time spent in proximity are taken to index high relationship quality. However, this formulation ignores the possibility that there are multiple reasons for affiliation. As discussed by Kummer (1978) and Cords & Aureli (1993), relationships can be characterised on at least three dimensions - value, security and compatibility. In Cords & Aureli's terminology, *value* refers to the benefits which can be derived from a relationship; *compatibility* to the accessibility of the partner - i.e. if they are often nearby in the group or have a history of friendly interaction; *security* to the predictability of a relationship - the degree to which an individual can expect its partner to behave in a particular fashion. This tripartite distinction recognises that an animal of high value may receive high rates of affiliation but that their partner may not perceive the relationship as a secure one. Clearly, to better describe primate relationships we require a measure of security. As security captures the predictability of relationships it can, in principle, be assessed by measuring how comfortable an individual is with a conspecific; assuming that individuals will be most comfortable or relaxed in the presence of partners whose behaviour is most predictable. Therefore, behavioural measures of an individual's emotional state could enable us to distinguish differing levels of security. Potentially, one such measure is that of self-directed behaviour (SDB). Scratching, self-grooming, self-touching, yawning, and body-shaking have been associated with tension and anxiety in non-human primates (reviewed by Maestripieri et al. 1992). In olive baboons, aggression increases SDB rate, while reconciliation reduces it (Castles & Whiten in press b), so SDB appears to index stress in this species.

In this chapter, I tested whether SDB could be used to measure relationship security by examining the effect of social proximity and dominance status on rates of SDB in wild olive baboons. 1) I expected that the close presence of conspecifics with whom an individual held an insecure relationship would be more likely to induce stress in a baboon than the close presence of individuals with whom he or she held a secure relationship. 2) Because dominant individuals present more danger than subordinates, on average, I expected relationships with higher ranking conspecifics to be less secure than those with lower ranking individuals. 3) Since SDB increases in stressful situations in this population, I predicted that close proximity with higher ranking individuals would be accompanied by higher rates of SDB than close proximity with lower rankers.

Methods

Study Site and Subjects

Details of the site and subjects can be found in Castles & Whiten (in press a).

Data Collection

Twenty animals were selected as subjects for 'focal animal samples' (Altmann 1974). At the beginning of focal sampling, these were 8 adult and 2 subadult females; 5 adult and 5 subadult males. All adult males (except Hk, who 'floated' between STT and MLK) were selected as subjects. Subadult males were selected so as to balance between natal and immigrant individuals (two new immigrants were excluded due to poor habituation). Adult females were divided into pairs of neighbouring rank according to a rank order constructed by T. Sambrook (Sambrook 1995) and one of each pair chosen at random. This procedure prevented the selection of pairs of known sisters. I selected two subadult females to balance the subadult males; both were older and reproductively active - Be became pregnant and gave birth during the study, and Tz was the focus of adult male consort activity. During the course of the study 5 male focal subjects left the troop; of

these two were replaced with animals as closely matched to them as possible, a third was replaced but subsequently returned to the troop and both he and his replacement were sampled until the replacement left the troop. The final emigrants left during the last fifth of the study so no replacements were selected. Table I has details of focal subjects.

Focal sampling began on 26 June 1994 and concluded on 7 April 1995. Each day was divided into one 3-hour and four 2-hour blocks: 0700-0900, 0900-1100, 1100-1400, 1400-1600, 1600-1800 hours. Focal animals were sampled once in each time block for each of ten months, or for as many of those months as they were in the troop. Animals were not sampled more than once in a day. To balance samples, we alternated observations between males and females and completed a full 'block' of all 20 subjects' samples before sampling an individual again. Focal samples were of 30 minute duration, except when interrupted (e.g. if the focal animal entered bush so thick as to make accurate observation impossible, or for very heavy rain) and were cancelled if the interruption lasted longer than 10 minutes. Samples of less than 20 minutes were discarded and the subject re-sampled at the next opportunity.

Focal samples were collected on a Hewlett-Packard 95LX hand-held computer running a modified version of the Mbuni event recorder program (Marsh 1992). Samples involved both continuous and instantaneous or 'point' recording (Altmann 1974).

Data on self-directed behaviour were recorded continuously. Definitions follow Schino et al. (1988):

Scratch - (usually repeated) movement of the hand or foot during which the digits are drawn across the fur or skin.

Self-groom & self-touching - picking through and/or slowly brushing aside fur with one or both hands. Brief self-touching included wiping eyes, inspecting feet and placing hand to mouth.

Body-shake - shaking movement of entire body (similar to that of a wet dog).

Yawn - brief gaping movement of the mouth. Not recorded as a SDB if accompanied by aggressive signals such as eye-flash or canine-whetting.

Scratching and self-grooming were scored as bouts of undefined duration. A break of at least 5 seconds, or a switch to another class of SDB, was required before scoring a new bout. Yawn and body-shake were scored on each occurrence. Whenever a SDB bout was scored, I recorded the identity of the nearest animal within 5 m of the focal animal (within 2 m at sleeping sites) or, if none, the identity of the nearest animal within 10 m.

Instantaneous samples were taken at the start of a focal observation and at one minute intervals thereafter. The identities of all animals within 5 m of the focal animal (within 2 m at sleeping sites) or, if none were within this range, the identity of the nearest animal within 10 m, was recorded.

During continuous and instantaneous sampling the presence of animals under 1.5 years of age was ignored.

Analysis

First, I constructed a troop dominance hierarchy from opportunistic records of dyadic displacement, avoidance and aggression. Polyadic data were included when a single individual displaced, was avoided by, or won a conflict against multiple others. We confirmed that the hierarchy was linear ($n = 68$, $h' = 0.457$, $p<0.001$) by employing de Vries's (1995) revised version of Appleby's (1983) procedure which compares the number of circular triads (reversals) in a matrix to the expected number of such triads, given random dominance relationships (de Vries's revision accounts for unknown and tied relationships). Table II represents the adult and sub-adult female portion of the hierarchy.

Next, for each focal individual I calculated the number of bouts of SDB performed per minute of focal observation (overall SDB rate). I then determined the number of point samples in which each of the other

Table I. Subjects for focal samples.

Sex	ID	Date of Birth	Adult	Residence [1]	Joined STT	Left STT	Reproductive State [2]	Months Sampled	Minutes Sampled
Females	Al		18/5/90	natal			L, C	July 94 - April 95	1490
	Am		23/9/91	natal			C, P, L	July 94 - April 95	1499
	Be	9/1/87	2/3/95	natal			C, P, L	July 94 - April 95	1500
	Cn		28/11/91	natal			L, C, P	July 94 - April 95	1497
	Dk		14/10/93	natal			C, P	July 94 - April 95	1500
	Es	Late 85	14/10/93	natal			L, C	July 94 - April 95	1493
	Jn		23/9/91	natal			P, L	July 94 - April 95	1500
	Ke		18/1/90	natal			C, P, L	July 94 - April 95	1500
	Ni		Before 86	natal°			C, P, L	July 94 - April 95	1500
	Tz	10/12/87	sub-adult	natal			C	July 94 - April 95	1499
Males	De			R	1/3/92			July 94 - April 95	1499
	Dj		1/11/92	LTR	1/4/89			July 94 - April 95	1499
	Gd	14/10/85	sub-adult	R	1/5/91*			July 94 - April 95	1494
	Gg	14/5/84	1/1/95	LTR	3/7/89*	5/3/95		Dec 94 - March 95	450
	Mi		sub-adult	natal				July 94 - April 95	898
	Mj	10/8/83	sub-adult	LTR	10/5/88*	8/12/94		July 94 - Dec 94	810
	Mx	17/6/86	sub-adult	natal				July 94 - April 95	1498
	Nk	Early 85	sub-adult	natal		27/10/94		July 94 - Oct 94	600
	Ra			R	1/7/93			July 94 - April 95	1500
	Si		1/10/87	LTR°	Before 86			July 94 - April 95	1499
	To	1/11/85	sub-adult	natal		6/3/95		July 94 - March 95	1230
	Vx		sub-adult	S	1/5/94			Dec 94 - April 95	677
	We		Before 86	LTR°	Before 86			July 94 - April 95	1407

1. Length of residence for immigrant males: S=Short term resident (< 1.5 year), R=Resident (1.5 - 5 years), LTR=Longest-term resident (> 5 years) at mid-point of study period (after Strum 1994). 2. C=Cycling, L=Lactating, P=Pregnant. * Gd & Gg initially entered STT on 26/4/89, Mj on 16/3/87; given dates mark beginning of permanent residence. ° Probable residence status: present in STT when troop was first followed.

Table II. Dominance hierarchy for adult and subadult females - June 1994 - April 1995. Derived from *ad libitum* observations of displacement, aggression and avoids. Numbers are totals of observed interactions, with the individual on the vertical axis scored as winner. Focal subjects are underlined.

ID	Es	Ma	Wt	Ke	Tu	Tz	Ky	Tt	Sc	St	Dk	Am	Dn	Gt	Cn	Be	Jn	Mo	Ln	Lz	Al	Tr	Ty	Ni	Ye
Es		10	14	19	7	9	23	7	10	6	1	7	5	6	8	1	4	3	1	6	4	2	3	4	
Ma			12	11	5	1	4	1	10	6	3	1	5	12	7	2	3		2	2	5	3	2	5	
Wt				10	6	15	6	1	9	6	10	4	7	9	7	2	6	1	3	2	2	2	3	7	
Ke					12	4	10	2	3	5	4	2	6	9	5	1	3	2	3	2	8	1	1		1
Tu							1	1	2	1	1	1	2	2		2	4		1	3		3		3	
Tz				1			6	4	13	3	2	6	2	6	17	6	4	6	5	1	3	2			
Ky								10	4	6		6	6	6	6	3	1	3	4	2	2	6	3	1	1
Tt									6		5	3			1	5		3	2	2	4			2	
Sc										2	13	2	1	7	11	3	4	1	3	5	3	3	1		
St											2	2	3	2	2	6	4	4	4	1	2	2	3	1	
Dk												7			9	3	2	5	4	8	6	1	2	5	1
Am									1				2	4	7	4	3	3	5	7	9	11	1	3	
Dn														4	4	4	3	2	1	5				3	1
Gt				1							3		1		4	4	6	1		2	3	3		1	
Cn																5	4	2	3	7	9	2	2	1	
Be																	2	3	6	3	8		3	2	
Jn		1																2	3	1	6	4	1	3	
Mo																			7	5	1		2		
Ln																				3	2		2		
Lz																					8	2		4	
Al																						3	3	4	1
Tr																							2	1	
Ty																									
Ni																									
Ye																									

individuals in the group was their nearest neighbour within 5 m and derived focals' SDB rates both when there was and when there was not another individual within 5 m. Having delimited the sample in this fashion, I calculated the rate of SDB associated with each near neighbour as follows. Let *s* be the number of bouts of SDB exhibited by the focal when individual *X* was nearest neighbour, and let *p* equal the number of point samples in which *X* was nearest neighbour. Then, for individual *X* the focal's near neighbour SDB rate (NNR) = *s* / *p*. Each point sample represents 1 min of co-presence so NNR is measured in SDB bouts per min.

To assess the effect of neighbour's dominance rank on focal SDB rate I selected only those individuals who had been the nearest neighbour within 5 m in at least 5 of the focal's point samples. This was intended to limit the distortion of results through selecting animals who were very rarely nearest neighbour. As individuals are expected to spend relatively small amounts of time in close proximity to individuals with whom they hold insecure relationships this should have reduced the chance of finding an effect of dominance on NNR. Finally, I used ANOVA to compare focal NNR when higher ranking individuals were nearest neighbour to focal NNR when lower ranking individuals were nearest neighbour. Analyses were two-tailed and the significance level was 5%.

As adult and sub-adult male focal subjects were all in the top third of the dominance hierarchy and infrequently spent time in close proximity, they were poor subjects for these analyses. Therefore, in this chapter, I analyse data from female focal subjects only. One female, Ni, could not be used for some analyses because, apart from a brief period in which a sub-adult female, Ye, immigrated into the group, she was at the bottom of the dominance hierarchy

Results

Mean overall SDB rate was 0.42 bouts per min (N=10; SD=0.08); Figure 1 has individual scores. On average, females had at least one individual of over 1.5 years of age as nearest neighbour in 62.9% of point samples

Figure 1

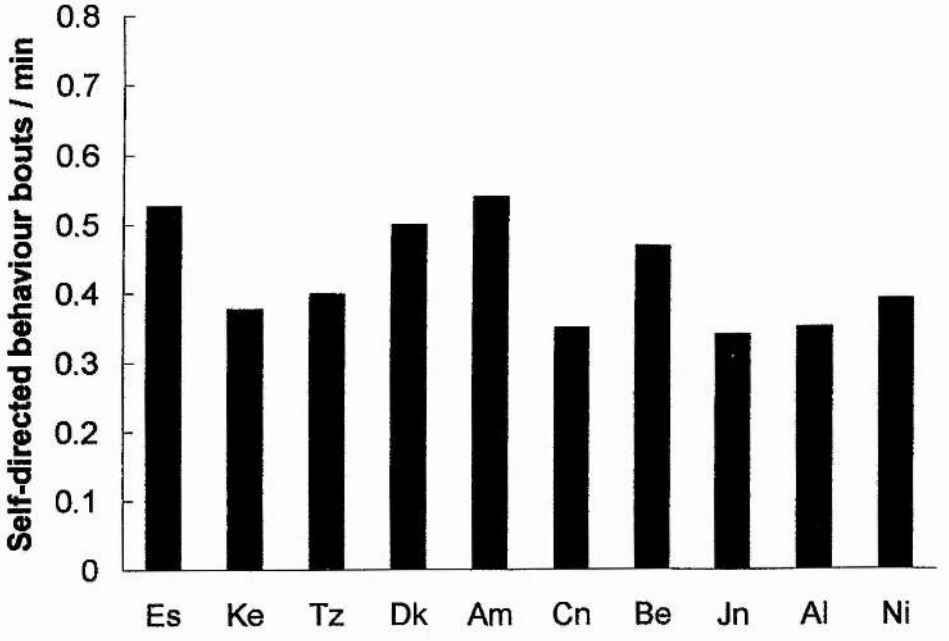

Figure 1. Combined self-directed behaviour (scratch + self-groom + body-shake + yawn) rates per min during focal observations. Female subjects are presented in order of dominance; alpha female at the extreme left.

(N=10; SD=4.8%). The number of such partners (as a percentage of total available partners) who were near neighbour in at least 1 point sample was 93.9% (N=10; SD=2.0%). The mean percentage of partners who were present on at least 5 occasions was 73.7% (N=10; SD=6.0%); figure 2.

For the nine females who possessed both higher- and lower-ranking partners, I calculated mean NNR when the near neighbour was higher-ranking and when the near neighbour was lower-ranking (for partners who had been near neighbours in at least 5 point samples; Fig. 3). I then ran an ANOVA with NNR as the dependent variable and subject and near neighbour dominance status as independent variables. When the focal's near neighbour was dominant NNR was significantly higher (mean=0.50 vs. 0.35 bouts / min; N=9, $F_{1,8}$=4.71, p<0.001). Restricting the analysis to female partners produced similar results (mean=0.53 vs. 0.33 bouts / min; N=8; $F_{1,7}$=6.57, p<0.001; Fig. 4).

Figure 5 presents baseline rates of SDB - the number of bouts of SDB when the focal had no nearest neighbour within 5 m divided by the number of point samples in which there was no nearest neighbour within that distance - alongside rates when the nearest neighbour was dominant or subordinate. There is no clear pattern to where baseline rate lies relative to dominant and subordinate NNR rate. However, in the majority of cases females' baseline rates are above subordinate NNR rate (7 of 9) and below dominant NNR rate (5 of 9). Baseline rates were significantly higher than overall rates (Wilcoxon signed ranks test: N=10, T=52, p<0.01) and significantly lower than rates of SDB when there was no nearest neighbour within 10 m (Wilcoxon signed ranks test: N=10, T=53, p<0.01).

Discussion

Sexually mature female olive baboons exhibited significantly higher rates of self-directed behaviour (a combined measure of scratching, self-grooming, self-touching, body-shaking and yawning) when their nearest neighbour (within 5 m) was a dominant conspecific than when he or she was a subordinate individual. The results support the hypothesis that SDB indexes

Figure 2

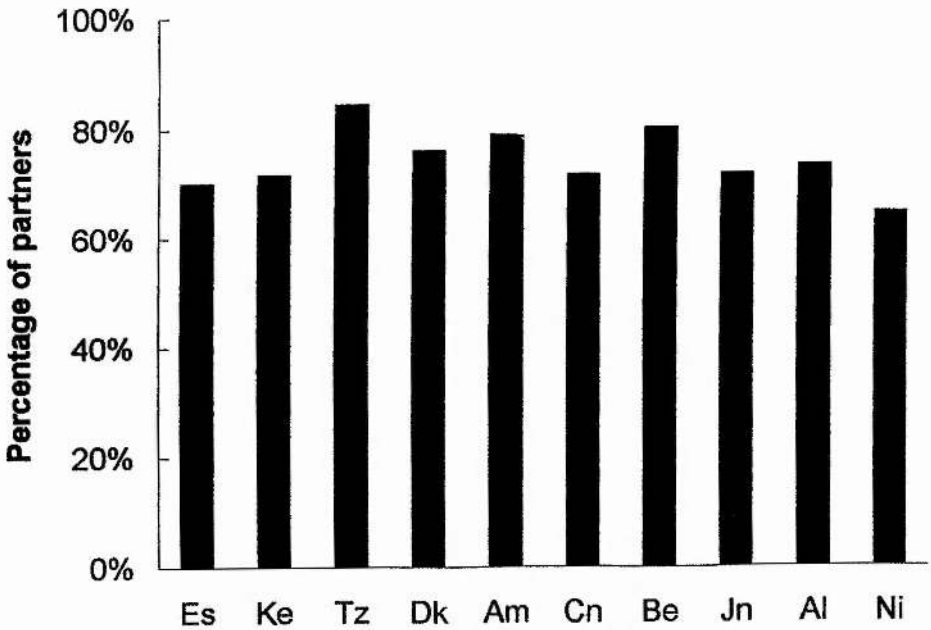

Figure 2. The proportion of conspecifics who were nearest neighbour (within 5 m) in at least five of each focal subject's point samples.

Figure 3

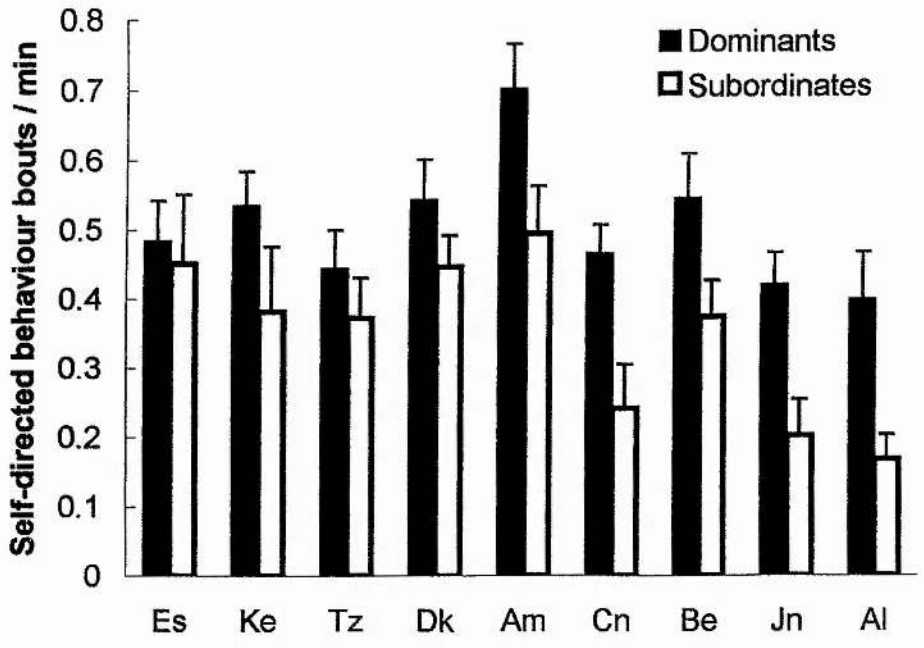

Figure 3. Self-directed behaviour rates (x ± SE) when a dominant or subordinate conspecific was nearest neighbour within 5 m.

Figure 4

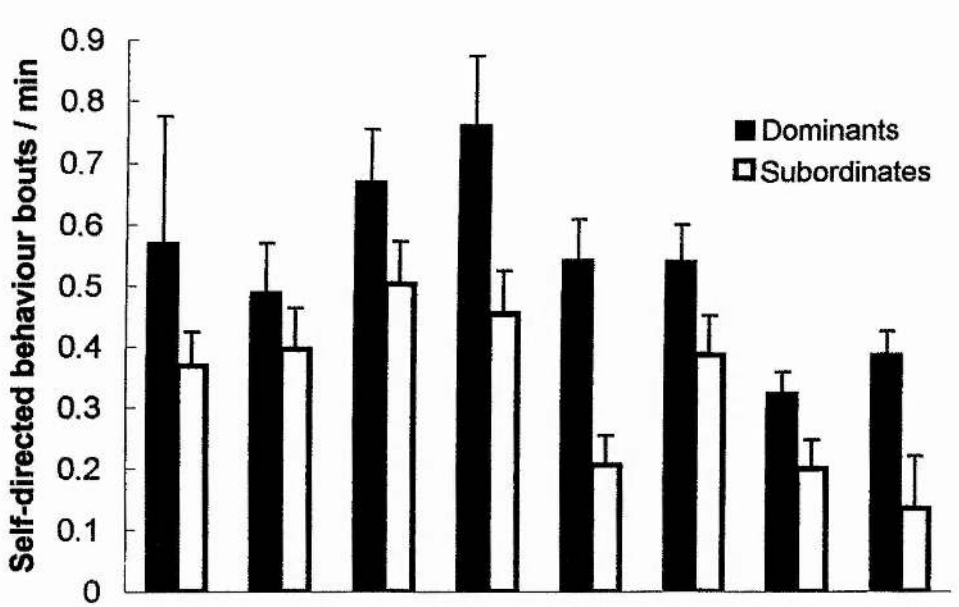

Figure 4. Self-directed behaviour rates (x ± SE) when a dominant or subordinate female conspecific was nearest neighbour within 5 m.

Figure 5

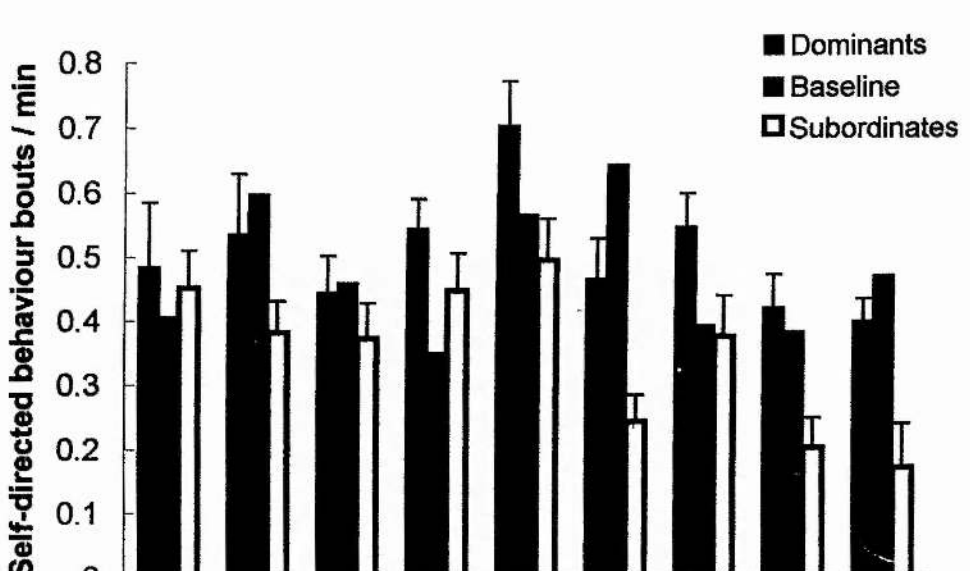

Figure 5. Self-directed behaviour rates (x ± SE) when a dominant or subordinate female conspecific was nearest neighbour within 5 m and when there was no nearest neighbour within 5 m (baseline rate).

stress in primates. Furthermore, they suggest that SDB can be used to index relationship security in this species.

As expected, female baboons' SDB varied predictably according to the dominance status of the baboon positioned closest to them in the group. Since aggression increased SDB and reconciliation reduced SDB in the same individuals, and those effects seem best explained by underlying levels of stress in combatants (Castles & Whiten in press b), the most parsimonious explanation of this near neighbour effect is that the close presence of dominant individuals leads to more frequent activation of the stress response (Sapolsky 1994) than the presence of subordinates. Activation of the stress response physiologically prepares an individual to respond to dangerous situations. In common with other cercopithecine primates, aggression among olive baboons is predominantly directed down the hierarchy (Smuts 1985; Strum 1987), thus the presence of a dominant individual will, for the most part, present more potential danger than the presence of a subordinate, and increased stress should be expected. The results clearly support this expectation.

In earlier studies, Troisi & Schino (1987) and Pavani et al. (1991) reported positive correlations between the frequency of self-grooming and the frequency of scratching and the proportion of time female long-tailed macaques spent within 1 m of the single adult male with which they were housed. This study radically extends these authors' methods and results by recording the identity of near neighbours when SDB occurred and directly relating variation in SDB rate to the presence of near neighbours; i.e. this study is not correlational. Furthermore, this study contrasts SDB response to a range of dominant and subordinate conspecifics while the earlier studies simply related displacement rates to a measure of how often the female subjects were in close proximity to a single dominant male. Finally, earlier studies were of captive animals in highly confined conditions, this study is of an unrestricted wild population.

An aspect of this study's results which merits discussion is the pattern of SDB behaviour seen when baboons had no near neighbour. Given the difference in danger posed by individuals of differing dominance status we

might expect 'no near neighbour rate' (NNNR) to lie between dominant NNR and subordinate NNR. However, while NNNR tended to be lower than dominant NNR its level was not usually intermediate to dominant NNR and subordinate NNR; in fact, NNNR tended to be relatively high. Yet, on further reflection, this may not be entirely surprising especially given that NNNR (when there was no near neighbour within 5 m) was significantly higher than overall SDB rate (the frequency of SDB over all focal observations regardless of the presence or absence of near neighbours). An explanation of this may be that stress has multiple causes. At some times, being detached from near neighbours is not a propitious situation for a baboon - such situations will include times when the animal is dangerously distant from near neighbours, increasing predation risk or separation from potential allies - and as such might induce stress. This argument is supported by an examination of SDB rate when the focal had no other baboon within 10 m; this rate was significantly higher than that when there was a baboon within 10 m but none within 5 m (NNNR).

However, for the purposes of measuring relationship quality, the critical comparison is that of dominant to subordinate NNR and here the results were clear cut. So, to what extent can SDB be used to assess relationship security? First, it should be noted that the measure of SDB used here does not directly map to 'relationship security' as defined by Cords & Aureli (1993), which emphasises the degree of predictability in a relationship, with high levels of unpredictability related to low levels of security. For example, a relationship marked by predictable aggression from the dominant individual would be regarded as secure by Cords & Aureli's definition. I would expect the subordinate in such a relationship to exhibit high rates of NNR and spend relatively little time near the dominant. To label this relationship as being insecure perhaps comes closer to the intuitive understanding of the term and therefore it seems appropriate to directly relate NNR to security: high NNR marking low security and low NNR, high security.

The advantage of NNR is that it provides some measure of *disposition* and in combination with affiliation measures has the potential to produce a

simple but multi-dimensional gauge of relationship state. NNR may also allow us to infer relationship value. To spell this out, if an individual directs affiliation equally as often towards two different partners but has different NNR with those two partners we can infer, because the level of security in the relationship with high NNR is lower, that this relationship is of higher value to the individual than it's relationship with the other. The reasoning here is that the individual is prepared to endure higher levels of stress to service the lower security relationship and, if the individual is investing economically, that relationship must promise or provide higher benefits to balance the elevated stress costs associated with it. This reasoning is very similar to that recently employed in animal welfare research where the value of a resource to an animal is assessed by observing how hard it will work (i.e. what costs it will accept) to obtain it (Dawkins 1993).

Such analyses should go beyond those attempted in this chapter. The next stage of research should examine affiliation and NNR in combination and attempt a characterisation of individual relationships. Here, I have only demonstrated differences across the broad relationship classification that is dominance/ subordination. While this is instructive, far more information on the nature of group organisation could be derived from a matrix detailing the patterns of NNR and affiliation, and from them details of the security and value of relationships among group members.

There are, though, some difficulties with employing SDB as a gauge of relationship security. One problem is that SDB is an intrinsically noisy measure. As already discussed, NNNR was higher than expected, probably reflecting multiple sources of stress in baboon life. Secondly, SDB should not be seen as a 'pure' measure of stress. Undoubtedly a proportion of any individual's SDB is not a product of stress but simple self-maintenance behaviour, particularly in an environment rich in ectoparasites. However, this need not be a critical difficulty as long as the stress 'signal' is stronger than the self maintenance 'noise', and as long as individuals are used as their own baseline for the detection of a stress signal. The results of this and other analyses plainly indicate that this problem is not insurmountable, at least in this population.

A further problem lies in assessing the relationship security of individuals who are rarely found in close proximity. In this chapter I concentrated on the behaviour of females because sexually mature males rarely affiliated or spent time close to each other. Like many other measures, NNR becomes less reliable if it is based on a limited sample. However, as NNR is designed as a measure of relationship security and a lack of affiliation, proximity, or active avoidance is indicative in itself of rather low security or, alternatively, low value this is not as great a problem as it may at first seem. Given that a large enough sample has been collected to give animals 'fair opportunity' to provide a reliable measure, the inability to obtain one indicates that those individuals possess a certain quality of relationship. It should also be noted that the distances employed for categorisation of near neighbour presence in this study were more or less arbitrary and in principle a broader sweep of the physical environment could draw in more individuals to the analysis.

Finally, with the formulation of NNR employed in this chapter the nearest neighbour is attributed with causing stress. This is clearly not always going to be correct; in fact we might expect an individual who is associated with high NNR to produce very similar levels of NNR if they are within 5 m of the focal regardless of whether they are actually the nearest neighbour or not. An obvious solution to this problem would be to record the identities of all, or if that proves impractical, more, of the individuals within close proximity to the focal when he or she is involved in SDB. NNR could then be calculated by dividing SDB when within close proximity of a given partner divided by time spent in close proximity to that partner. This measure should give a clearer picture still of which conspecifics are most often associated with high NNR.

Chapter 7. CONCLUDING DISCUSSION

Introduction

In this final chapter, I summarise the results presented in this thesis and briefly discuss some of the key points arising from these results.

Overview of results

Reconciliation was demonstrated in two large groups of pigtail macaques. In both groups former opponents were selectively attracted to each other in the immediate post-conflict period. Characteristics and dimensions of social relationships, such as kinship and level of affiliation, affected conciliatory tendency. In Old group, kin reconciled their conflicts more often than non-kin. In both groups, conflicts were more frequently reconciled between opponents whose relationships were characterised by high levels of affiliation.

The groups did differ in other aspects of their conciliatory behaviour: First, only in the more recently established group (New) were recipients of aggression more likely to initiate reconciliation. Second, only in the long-established group (Old) was the distribution of specific affiliative acts during post-conflict reunions significantly different from the distribution during matched control period interactions. More importantly, Old group individuals were twice as likely to reconcile their conflicts as those of New group, yet there was no significant between-group difference in individual expression of other social variables such as time spent allogrooming, and the direction and frequency of approaches and aggression. Individuals of Old group did, however, affiliate with significantly fewer conspecifics, distributing this affiliation less evenly. They, thus, seemed to have more concentrated, less egalitarian social networks than New group animals.

Reconciliation was also demonstrated in a population of wild olive baboons. Mean conciliatory tendency was 15.6%, indicative of a relatively intolerant dominance style. Reconciliation was particularly infrequent when one of the combatants had been eating or foraging just before aggression

began. In contrast, neither the directionality nor the decidedness of the original conflict significantly affected reconciliation frequency. However, aspects of the relationship between combatants were related to variation in conciliatory tendency: close kin were more likely to reconcile conflicts than more distantly or unrelated individuals, while individuals close together in the dominance hierarchy also reconciled relatively often. Aggression affected the activity budget of combatants: aggressors were more likely to forage after conflicts while victims spent more time travelling.

In contrast to their behaviour toward former opponents, neither victims nor aggressors were any more likely to become involved in affiliative interactions with non-combatants in post-conflict periods than they were in baseline periods. However, there was evidence that both victims and aggressors more frequently affiliated with the kin of former opponents following aggression. Affiliation rates with individuals who had supported them in the original conflict also increased. Redirection of aggression to uninvolved individuals by victims was rare, though, and it did not occur any more regularly than in control periods.

Olive baboons, regardless of sex or their role in the initial conflict, suffered a clear stress response in the period following a conflict, indexed, in this case, by strongly elevated rates of scratching, autogrooming, yawning and body-shaking. Neither the intensity nor the context of the conflict significantly altered this response which would appear to be an adaptation enabling baboons to physiologically prepare for involvement in further aggression, rates of which were also elevated in the immediate post-conflict period. Moreover, if former opponents interacted affiliatively in the first few minutes of the post-conflict period, their SDB rate rapidly fell to a level akin to that observed in periods without aggression. Reconciliation also reduced the likelihood of becoming involved in further aggression with former opponents and other troop members.

Adult and subadult female olive baboons uniformly exhibited significantly higher rates of self-directed behaviour when their nearest neighbour (within 5 m) was of higher dominance rank than when he or she was a subordinate individual. The results again indicate that SDB is related

to stress and that SDB can be used to index relationship security in primates.

Reconciliation and relationships

The most important result of the comparison of the two pigtail macaques groups was that variation in the nature of inter-individual relationships provided the best explanation of a marked between group difference in reconciliation frequency. Individuals of Old group had restricted affiliative networks and spent more time engaged in affiliation with their most preferred social partners than individuals in New group. They also reconciled conflicts with those preferred partners at very near to double the frequency of the equivalent pairs in New group. These results clearly support the hypothesis that reconciliation will be most common among individuals with the highest relationship quality and that reconciliation has evolved to ameliorate the damage inflicted on relationships by aggression (e.g. de Waal 1989b; Cords & Aureli 1996). The direct link of relationship investment to variation in the expression of reconciliation across primates groups is a unique result which merits comparable investigation in other species. The analysis strategy developed in this study is currently being utilised to compare relationship quality and conciliatory tendency across an extended macaque database (de Waal, Call, Castles & Aureli in preparation).

The results of Chapter 4 further reinforce the link between relationship quality and reconciliation frequency. Apart from the impact of foraging in greatly diminishing the likelihood of reconciliation the only factors which had any significant association with conciliatory tendency were those relating to aspects of the relationship between combatants. The presence of a young infant makes mothers more attractive to partners thus increasing their social value (Altmann 1980; Maestripieri & Wallen 1995). Similarly, individuals are expected to value their relationships with kin relations or those of similar rank to themselves (Dunbar 1988). All three factors were predictive of higher conciliatory tendency.

Uncertainty Reduction

The results of Chapter 5 are important for at least two reasons. First, they demonstrate that the stress-related behaviour of wild baboons closely parallels that observed in captive macaques (Aureli et al. 1989; Aureli & van Schaik 1991b; Aureli in press; de Waal & Aureli in press). Rates of stress-related behaviour increased shortly after the conclusion of a conflict but were restored to baseline levels upon the occurrence of post-conflict affiliation between the former opponents. This strongly suggests that the same proximate mechanism of uncertainty reduction attributed to captive macaques (Aureli & van Schaik 1991b) operates in wild baboons; a different species living in a different environment with very different constraints. Secondly, the results extend the scope of the uncertainty reduction hypothesis to aggressors and are indicative of some interesting phenomena. Though it should be noted that these results are somewhat compromised by the very small data sets from which they are derived, they deserve to be pursued with larger samples and in different populations.

Self-directed behaviour and relationship quality

Having established that self-directed behaviour indexed stress in this population, Chapter 6 tested some of the dimensions of SDB expression outside the context of aggression. A particular aim was to test the utility of SDB as an easy to collect measure of relationship security. The chapter took initial steps in this direction by demonstrating that dimensions of the relationship between two individuals affect the expression of SDB when those individuals are in close proximity, and do so in a predictable manner. Clearly there is considerable scope for further work to be done in this area. In particular, the next step should involve the conjunction of affiliation rate with the near neighbour rate index of relationship security to develop matrices in which measures of relative security and affiliative investment are considered simultaneously. Such matrices could then be used descriptively to detail and compare the distributions of affiliation and relationship security within and between primate groups. They could also be correlated with other

variables, for example aggression and reconciliation rates, to clarify the association between relationship status and the expression of these, and other, behaviours.

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Appendix 1. Social interactions recorded continuously during Standard and PC / MC focal samples.

Class	Behaviour	Description
Affiliative	Brief contact	- other brief affiliative contact; less than 5 s.
	Come-hither	- chin pulled back and eyes narrowed.
	Copulate	- mounting with thrusting and/or intromission.
	Embrace	- placing arm around partner's shoulder or torso.
	Genital inspect	- inspection, including smelling, of partner's ano-genital region.
	Grooming	- allo-grooming: manipulation, brushing, or licking the fur, skin or eyes of another animal.
	Grunt	- grunting. Only scored if reciprocal or clearly directed.
	Hold bottom	- standing over partner with hands on their hindquarters.
	Huddle	- stationary, seated contact, other than allo-grooming, with another animal for at least 5 s.
	Infant affiliation	- contact affiliation with a dependent infant (< 1.5 years); infant off mother.
	Infant handle	- gentle contact with infant. Infant in contact with its mother
	Long contact	- stationary, non-seated contact; over 5 s.
	Non-sexual mount	- mounting without thrusting or intromission
	Passing contact	- apparently incidental contacts made during a slow-moving pass.
	Play	- social play. 15 s interruption required to score a further bout.
	Present	- orientation of ano-genital region toward another animal.
	Smell touch	- muzzle-muzzle contact
	Tail wrap	- wrapping tail around partner's body.
Ambivalent or Negative	Attempted play	- invites or begins unreciprocated play bout.
	Attempted genital touch	- as for genital touch but partner avoids contact.
	Avoid	- movement from the path of an individual before that individual gets within 0.5 m accompanied with glancing towards the approacher.
	Back-bite	- Crouching over partner's hindquarters and biting back in ritual fashion; unaccompanied by facial or vocal threat.
	Bare teeth	- facial expression in which teeth are bared by tightly pulling back face muscles.
	Genital touch	- male-male genital handling; reciprocal or unilateral.
	Infant grab	- rough contact with infant. Infant in contact with its mother
	Rough behaviour	- pushing, pulling or dragging partner; unaccompanied by facial or vocal threat.
	Side-bite	- ritualised biting similar to back-bite.

Appendix 2. Agonistic interactions recorded *ad libitum* and continuously during Standard and PC / MC focal samples. For each opponent, the highest intensity of aggression performed during an interaction (interval of at least 30 s for new interaction) was recorded. All supporters, all responses to aggression, and an outcome were recorded. Context was recorded when appropriate and observed.

Class	Behaviour	Description
Aggression	Intensity 1	- threats with facial and/or vocal components. Includes eye-brow flash and open-mouth 'pointing'.
	Intensity 2	- lunges of less than 2 m.
	Intensity 3	- chases of at least 2 m.
	Intensity 4	- intensity 3 plus contact.
	Intensity 4a	- 'aggressive holding': Forced restraint of an opponent. Victim is held to the ground while screaming for at least 5 s.
	Intensity 4g	- 'grappling': Bi-directional wrestling conflict, usually between males.
	Intensity 5	- brief biting. Strong grip of the skin/limb with the teeth for less than 5 s.
	Intensity 6	- fierce biting: Potentially or actually damaging. Biting sustained for more than 5 s, and/or accompanied by head shaking, and/or resulting in injury.
Response to aggression	Counter-aggression	- Intensity 1-6, as above.
	Flight	- rapid movement away from opponent.
	Submission	- teeth-baring or gecking.
	Vocalisation	- screaming and enlist-screaming. Enlist-screaming is higher-pitched, of longer duration and accompanied by looking for potential supporters.
	Withdrawal	- movement of more than one step away from opponent.
Support	Focal's supporters	- individuals who support the focal animal during the agonistic incident by directing aggression toward the opponent.
	Opponent's supporters	- individuals who support the focal's opponent during the agonistic incident by directing aggression toward the focal.
Outcome	Win	- focal's opponent unilaterally withdraws, flees or submits at the end of the conflict.
	Loss	- focal unilaterally withdraws, flees or submits at the end of the conflict.
	Draw	- no clear signs of submission shown by either opponent or no clear winner could be determined.
Context	Consort	- one or more opponent was involved in a consortship.
	Food	- conflict results in victim losing food source.
	Infant	- one or more opponent carrying a dependent infant.
	Redirection	- victim attacks a third, previously uninvolved, individual.
	Social	- one or more opponent was involved in social interaction.

Appendix 3. Activities recorded instantaneously during Standard and PC / MC focal samples.

Class	Behaviour	Description
Forage	Drink	- drinking.
	Eat[1]	- processing or eating food from a clumped food source.
	Forage[1]	- handling or eating from a dispersed food source.
Movement	Travel	- moving rapidly in a certain direction.
	Travel & search	- moving while scanning environment for food.
Social	Aggression[2]	- involved in aggressive interaction as defined in Appendix 2.
	Grooming[2]	- performing or receiving allo-grooming, as defined in Appendix 1.
	Social	- playing, copulating, huddling or involved in brief affiliative interaction, as defined in Appendix 1.
Visual	Attending	- immobile and visually alert though focus is unclear.
	Attending social	- as above but focus of attention clearly is a social interaction.
	Attending to intertroop	- as above but focus is a social interaction in, or a member of, another troop.
	Attending environmental	- as above but focus is a non-social feature, e.g. predator, local people, potential food source.
Other	Resting	- inactive and not visually attending. Also, includes self-grooming and eating from cheek pouches.
	Other	- other activity.

1. Eat and forage were accompanied by a code indicating the food source being eaten, handled or processed. Categories were subterranean, grass, herb, herb flower, herb berry, succulent, succulent fruit, mineral, shrub, shrub flower, shrub fruit, shrub bark, shrub thorn, tree, tree flower, tree thorn, tree bark, invertebrate animal, vertebrate animal, eggs. 2. Separate codes for performed and received.